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Front cover: Leptothecate hydroid colonies, *Lytocarpia angulosa* (left) and *Nemertesia cylindrica* (right), from Darwin Harbour
(From J. E. Watson, pages 1-82)



The Beagle

RECORDS OF THE MUSEUMS AND ART GALLERIES
OF THE NORTHERN TERRITORY

Volume 16, December 2000

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Hydroids (Hydrozoa: Leptothecatae) from the Beagle Gulf and Darwin Harbour, northern Australia

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ABSTRACT

Sixty-three species of leptothecate hydroids including 12 new species and six new records for Australia are reported from three collections (one dredging and two SCUBA diving) made in the Beagle Gulf and Darwin Harbour in the Northern Territory of Australia. Large, visually dominant hydroid colonies from reef and soft bottom include known species with distributional ranges throughout the Indo-Pacific, Indonesia and the Timor Sea. The systematic status of several poorly known species is reviewed and ecological observations used to unravel past confusion of several species. The preferred and possibly obligatory habitat for many species is the tubiculous polychaete worm *Eunice tubifex*.

KEYWORDS: Hydroids, Leptothecatae, Beagle Gulf, Darwin Harbour, northern Australia.

INTRODUCTION

This is the second report on hydroids collected from the Beagle Gulf and environs of Darwin Harbour in the Northern Territory of Australia. The first paper (Watson 1999) described the anthoathecate hydroids; this paper describes the leptothecate hydroids. The Beagle Gulf is a large, open embayment of the northern Australian mainland facing the Timor Sea between Melville and Bathurst Islands; Darwin Harbour lies on an inlet of the Beagle Gulf (Fig. 1). A description of the physical regime of the Beagle Gulf and environs of Darwin Harbour is given in Watson (1999).

Leptothecate species reported in this paper are derived from three separate collections: a major dredging survey of the invertebrate fauna of the Beagle Gulf undertaken in 1993 by the Parks and Wildlife Commission of the Northern Territory (formerly Northern Territory Conservation Commission) and two collections made in the environs of Darwin Harbour in August-September 1998 and in September 1999, the latter two collections being made by the author and others using SCUBA. Underwater collections in the environs of Darwin were made on reefs 1 km off East Point (EP), Plater Rock, 1 km offshore from Talc Head (PR), from the breakwater and channel bed off the East Arm Port (EA) and on wharf piles and port structures in the Port of Darwin (PD). These collections from hard substrate augment the Beagle Gulf collection which was dredged from predominantly soft bed. While the collections upon which this report and Watson (1999) are based have

considerably increased knowledge of the hydroid fauna in the Beagle Gulf, future collecting will certainly add more species to the faunal list.

Materials and methods of collection are given in Watson (1999). Station number, locality, depth and date of sampling in the Beagle Gulf Survey from which hydroids were recovered are listed in Table 1. Species and sites of collection are listed in Table 2. A taxonomic index is provided as Appendix 1. Type and voucher specimens are lodged in the Museums and Art Galleries of the Northern Territory, Darwin (NTM C) and the Museum of Victoria, Melbourne (MV F).

Eighty-three of the 162 stations occupied in the Beagle Gulf Survey yielded leptothecate hydroids. Of the 63 leptothecate species recorded in this study, 12 are described as new, five of these being collected by SCUBA diving in the environs of Darwin Harbour and six species are new records for Australia. Twenty-two, 20 and 19 species were recorded from three Beagle Gulf stations (Stns 136, 154, 87 respectively). These stations were among those sampled furthest from land, but apart from this geographical relationship they appear to share no common environmental features, the bed ranging from coarse sand at -6 m (Stn 87), rocky bottom at -30 m, (Stn 154) and a sponge bed at -18 m (Stn 136). Species recorded at these stations include *Macrorhynchia phoenicia*, *Idiellana pristis*, *Thyrosocyphus torresii*, *Plumularia scabra*, *Plumularia badia*, *Nemertesia cylindrica*, *Lytocarpia angulosa*, and *Gymnangium longicorne*. These species were also the most visually dominant seen in the two extensive SCUBA surveys in the environs of Darwin Harbour. Underwater

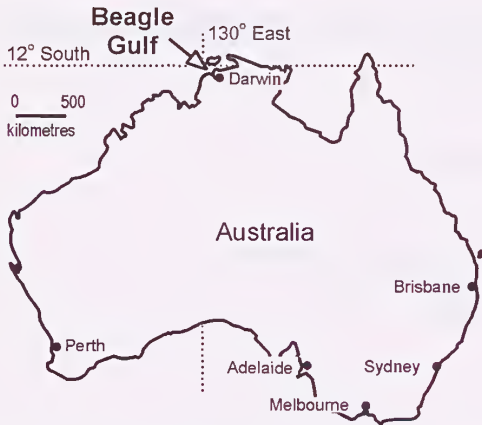


Fig. 1. Map of mainland Australia showing location of Beagle Gulf and Darwin.

observations in the environs of Darwin Harbour found that some other species (e.g. *Sertularella diaphana*, *S. quadridens*, *Gymnangium hians*, *Aglaophenia delicatula*, *Macrorhynchia philippina* and *Thyroscyphus fruticosus*) as well as several new species, were much more abundant than indicated by the dredged material. The only well represented species in the Beagle Gulf Survey collection not seen in Darwin Harbour was *Salacia sinuosa*.

Most of the previously known species range throughout the Indo-Pacific, Indonesia and the Timor Sea; many have circumtropical affinities extending to the Suez area, the Mediterranean Sea and the West Indies. Two (*Thyroscyphus macrocytharus*, *Salacia sinuosa*), are endemic to tropical and subtropical Australia. *Kirchenpaneria irregularis* and *Monothecha flexuosa* are known only from Australia and South Africa while *Fillellum serratum*, *Antennella secundaria* and *Plu-*

Table 1. Beagle Gulf stations from which leptothebate hydroids were recovered.

Stn No.	Locality	Depth m	Substrate	Date sampled
7	N of Cape Ford, Anson Bay, 13° 25.08'S, 129° 53.94'S	13	Sand, shale, coral rubble	1/10/1993
9	NE of Cape Ford, Anson Bay 13° 25.02'S, 129° 55.98'E	16	Sine sandy mud	1/10/1993
13	NNE of Cape Ford, Anson Bay 13° 22.14'S, 129° 53.40'E	24	Sandy mud	2/10/1993
17	Anson Bay, 13° 21.96'S, 130° 4.98'E	12	Mud	2/10/1993
20	N of Cape Ford, Anson Bay, 13° 19.14'S, 129° 56.28'E	29	Coarse sand and shale	2/10/1993
21	W of Daly River mouth, Anson Bay, 12° 19.14'S, 129° 59.16'E	31	Mud	2/10/1993
26	S of Bateman Shoal, Anson Bay, 13° 16.08'S, 129° 55.82'E	23	Coarse sand, shale and gravel	3/10/1993
27	SE of Bateman Shoal, Anson Bay 13° 15.90'S, 129° 58.86'E	19	Coarse sand	3/10/1993
32	E of Batemen Shoal, Anson Bay, 13° 12.96'S, 129° 59.10'E	13	Rocky bottom	3/10/1993
33	S of North Peron Island, Anson Bay, 13° 13.26'S, 130° 1.92'E	9	Coarse sand and shale	3/10/1993
35	E of South Peron Island, 13° 12.84'S, 130° 7.98'E	6	Coarse sandy mud and shale	2/10/1993
36	W of North Peron Island, Anson Bay, 13° 10.26'S, 129° 55.62'E	15	Coarse sand and shale	3/10/1993
38	Channel Point to North Peron Island, 13° 9.24'S, 130° 5.52'E	20	Gravel	3/10/1993
40	W of North Peron Island, 12° 6.96'S, 129° 58.86'E	8	Mud and rock	3/10/1993
48	NNE of North Peron Island, 13° 0.96'S, 130° 4.98'E	13	Mud, shale and sand	4/10/1993
49	N of North Peron Island, 12° 57.90'S, 130° 1.92'E	16	Mud	4/10/1993
50	NNE of Point Peron, 12° 57.96'S, 130° 4.98'E	10	Sandy mud	4/10/1993
52	E of Point Blaze, Fog Bay, 12° 54.96'S, 130° 7.98'E	7	Mud and shale	4/10/1993
53	E of Point Jenny, Fog Bay, 12° 54.78'S, 130° 14.16'E	4	Sandy mud	4/10/1993
54	E of Point Jenny, Fog Bay, 12° 54.96'S, 130° 15.60'E	4	Sandy mud	4/10/1993
56	NW of Blaze Reef, Fog Bay, 12° 52.02'S, 130° 11.10'E	6	Coarse sand and shale	4/10/1993
57	E of Blaze Reef, Fog Bay, 12° 51.96'S, 130° 14.10'E	7	Mud and shale	4/10/1993
58	W of Finnis River, Fog Bay, 12° 7.02'S, 130° 56.10'E	7	Fine mud	4/10/1993
61	W of Five Mile Beach, Fog Bay, 12° 49.92'S, 130° 19.38'E	7	Fine mud	5/10/1993
66	Bynoe Harbour, 12° 41.88'S, 130° 36.30'E	8	Sponge bed	7/10/1993
67	Bynoe Harbour, 12° 70.92'S, 130° 33.12'E	9	Coarse sand and shale	7/10/1993
69	SW of Dun In Mirrie Island, Fog Bay, 12° 40.02'S, 130° 19.92'E	6	Mud	5/10/1993
74	Bynoe Harbour, 12° 36.96'S, 130° 32.04'E	26	Coarse sand and shale	7/10/1993
77	W of Unjin Point, Port Patterson, 12° 33.60'S, 130° 27.90'E	16	Sandy mud and gravel	6/10/1993
78	E of Unjin Point, Bynoe Harbour, 12° 34.02'S, 130° 32.04'E	28	Coarse sand, shale and gravel	7/10/1993
80	NW of Roche Reef, Grose Islands, 12° 31.02'S, 130° 17.22'E	17	Coarse sand, shale and gravel	5/10/1993
81	N of Bass Reef, Grose Islands, 12° 31.02'S, 130° 20.04'E	15	Gravel and sponges	5/10/1993
82	W of Quail Island, Grose Islands, 12° 30.96'S, 130° 22.92'E	9	Coarse sand and gravel	6/10/1993
84	E of Moira Reef, Bynoe Harbour 12° 31.20'S, 130° 31.74'E	11	Coarse sand and gravel	6/10/1993
85	N of Bass Reef, Bynoe Harbour, 12° 27.96'S, 130° 20.16'E	19	Coarse sand, shale and mud	6/10/1993
87	S of Fish Reef, Grose Islands, 12° 27.90'S, 130° 26.70'E	6	Coarse sand	6/10/1993
88	W of Middle Reef, Bynoe Harbour, 12° 28.02'S, 130° 28.98'E	38	Mud, gravel and rock	6/10/1993
89	Middle Reef, Bynoe Harbour, 12° 28.80'S, 130° 32.10'E	14	Mud and gravel	7/10/1993
91	NW of Fish Reef, Grose Islands, 12° 25.44'S, 130° 25.92'E	19	Mud and gravel	6/10/1993

mularia setacea are temperate and tropical cosmopolitan species. Seven, mostly small and inconspicuous species (*Hebella ?laterocaudata*, *Anthohebella parasitica*, *Sertularella decipiens*, *Halopteris plagiocampa*, *Plumularia bedoti*, *Clytia ?warreni*, *Clytia linearis*) are new to the tropical Australian region.

Abundant material and diving observations of previously unknown habitat preferences, habit and colour of colonies served to differentiate between several species which in the past have been confused or considered to be variants of known species. Ample material from the diving surveys has also provided a basis for

review of the systematic status of several poorly known species.

Many of the species reported in this paper were found on the tubes of the polychaete worm *Eunice tubifex* Crossland, 1904. The tough mucilaginous tubes which stand erect to a height of c. 30 cm, occur abundantly on reef and man-made structures throughout Beagle Gulf and Darwin Harbour. The tubes provide a more or less sediment-free substrate for a diverse invertebrate community of small compound ascidians, bryozoans, sponges and hydroids. *Eunice tubifex* is a preferred and possibly obligatory habitat for several hydroid species.

Table 1 (cont.). Beagle Gulf stations from which leptotheate hydroids were recovered.

Stn No.	Locality	Depth m	Substrate	Date sampled
92	E of Fish Reef, Bynoe Harbour, 12° 24.84'S, 130° 28.92'E	17	Coarse sand and gravel	6/10/1993
93	Thrings Channel, Bynoe Harbour, 12° 24.96'S, 130° 31.98'E	29	Shale	7/10/1993
95	Charles Point, 12° 21.90'S, 130° 31.92'E	15	Gravel and sponges	7/10/1993
97	NE of Charles Point, 12° 21.84'S, 130° 37.86'E	14	Coarse sand and shale	7/10/1993
100	N of Nightcliff, Darwin Harbour, 12° 21.18'S, 130° 50.40'E	5	Muddy sand and seagrass	12/10/1993
101	WNW of Charles Point, 12° 19.02'S, 130° 34.02'E	19	Sand, gravel and mud	7/10/1993
104	Darwin Harbour, 12° 19.08'S, 130° 43.92'E	15	Fine sandy mud	13/10/1993
105	Outer Darwin Harbour, 12° 19.02'S, 130° 47.10'E	15	Mud, sand, shale and seagrass	12/10/1993
106	Outer Darwin Harbour, 12° 18.08'S, 130° 50.40'E	12	Mud, gavel and shale	12/10/1993
110	Outer Charles Point, 12° 15.84'S, 130° 37.86'E	27	Sandy mud	13/10/1993
111	Outer Charles Point, 12° 16.08'S, 130° 40.98'E	28	Sandy mud	13/10/1993
113	Outer Darwin Harbour, 12° 15.84'S, 130° 47.22'E	20	Sandy mud and shale	12/10/1993
114	Outer Darwin Harbour, 12° 16.08'S, 130° 50.04'E	18	Mud, gravel and shale	12/10/1993
115	N of Lee Point, Shoal Bay, 12° 16.02'S, 130° 53.04'E	16	Mud and shale	11/10/1993
116	Shoal Bay, 12° 15.96'S, 130° 55.86'E	13	Sandy mud and seagrass	12/10/1993
118	Fenton Patches, Darwin Harbour, 12° 13.08'S, 130° 44.04'E	20	Coarse sand and shale	12/10/1993
119	Outer Darwin Harbour, 12° 12.90'S, 130° 47.04'E	23	Mud	12/10/1993
120	Outer Darwin Harbour, 12° 13.02'S, 130° 50.04'E	22	Coarse sand, shale and mud	12/10/1993
121	Shoal Bay, 12° 13.02'S, 130° 52.92'E	19	Mud	12/10/1993
122	Shoal Bay, 12° 13.08'S, 130° 55.98'E	17	Sandy mud and seagrass	12/10/1993
126	Outer Darwin Harbour, 12° 10.08'S, 130° 46.92'E	30	Mud and gravel	12/10/1993
127	Outer Darwin Harbour, 12° 10.02'S, 130° 49.86'E	27	Muddy sand, shale, sponges	12/10/1993
129	W of Gunn Point, Shoal Bay, 12° 09.96'S, 130° 59.76'E	15	Gravel	
131	Mouth of Leaders Creek, Shoal Bay, 12° 9.36'S, 131° 8.32'E	4	Sandy mud	10/10/1993
132	NE of Stephens Point, Adam Bay, 12° 10.02'S, 131° 11.40'E	4	Sandy mud, shale and gravel	10/10/1993
136	Outer Shoal Bay, 12° 6.90'S, 130° 49.92'E	18	Sponge bed	12/10/1993
137	SW of Marsh Shoals, outer Shoal Bay, 12° 7.02'S, 130° 52.92'E	20	Sponge bed	12/10/1993
138	S of Marsh Shoal, Vernon Islands, 12° 7.02'S, 130° 56.10'E	16	Gravel	11/10/1993
139	SSE of Lyne Reef, Vernon Islands, 12° 7.08'S, 130° 59.04'E	30	Shale and rock	11/10/1993
140	W of South West Vernon Island, 12° 6.90'S, 131° 4.80'E	13	Coral rubble	10/10/1993
144	W of Ruby Island, Chambers Bay, 12° 7.08'S, 131° 20.04'E	22	Shale and coral rubble	
146	N of Marsh Shoal, Vernon Islands, 12° 4.02'S, 131° 55.86'E	39	Rocky bottom	10/10/1993
147	SW of North West Vernon Islands, 12° 4.02'S, 131° 58.86'E	16	Shale and gravel	10/10/1993
148	S of North West Vernon Island, 12° 3.96'S, 131° 1.92'E	25	Rock	10/10/1993
149	E of East Vernon Island, 12° 4.98'S, 131° 8.40'E	26	Gravel, shale and sand	10/10/1993
150	Rooper Reef, Vernon Islands, 12° 3.96'S, 131° 11.10'E	22	Gravel	10/10/1993
152	W of Elizabeth Reef, Cape Hotham, 12° 4.02'S, 131° 20.04'E	21	Shale	9/10/1993
153	E of Dryston Reef, Cape Hotham, 12° 4.08'S, 131° 22.80'E	6	Sponge bed	9/10/1993
154	N of Oliver Reef, Vernon Islands, 12° 1.02'S, 130° 58.86'E	30	Rocky bottom	11/10/1993
155	N of North West Vernon Island, 12° 1.02'S, 131° 1.86'E	38	Shale and gravel	11/10/1993
156	W of Knight Reef, Vernon Islands, 12° 1.20'S, 131° 3.96'E	22	Coarse sand, shale and rocks	11/10/1993
157	NW of Knight Reef, Vernon Islands, 12° 1.44'S, 131° 8.04'E	14	Gravel	10/10/1993
159	NW of Cape Hotham, 12° 1.32'S, 131° 13.92'E	34	Coarse sand and shale	9/10/1993
160	North of Cape Hotham, 12° 0.96'S, 131° 16.92'E	29	Sand, shale, gavel, sponges	9/10/1993
161	SE of Cape Hotham, 12° 0.96'S, 131° 19.86'E	22	Coarse sand and shale	9/10/1993
162	N of Dayton Reef, Cape Hotham, 12° 0.12'S, 131° 22.74'E	12	Mud and shale	9/10/1993

Table 2. List of species and sampling sites. Numerals represent Beagle Gulf Survey station numbers. SCUBA sampling sites in Darwin Harbour are: EA = East Arm Port breakwater and channel, PD = Port of Darwin wharves, EP = East Point reefs, PR = Plater Rock, off Talc Head.

Species	Sampling Sites
<i>Lafoeina amirantensis</i> (Millard and Bouillon, 1973)	38, 146
<i>Filellum ?serratum</i> (Clarke, 1879)	121, PR
<i>Hebellopsis costata</i> (Bale, 1884)	7, 8, 13, 38, 40, 53, 57, 80, 85, 136, 137, 140, 146, 159, PD, EA, PR
<i>Hebellopsis scandens</i> (Bale, 1888)	20, PD, EA, PR
<i>Hebella ?laterocaudata</i> Billard, 1942	139
<i>Anthohebella parasitica</i> (Ciamician, 1880)	7, 13, 33, 38, 40, 53, 137, 146, 159, PR
<i>Anthohebella darwinensis</i> sp. nov.	EA
<i>Halecium dyssymetrum</i> Billard, 1929	40, EP
<i>Halecium spatulum</i> sp. nov.	40, 48, PD.
<i>Hydrodendron dichotomum</i> (Allman, 1888)	138, PD, PR
<i>Diphasia mutulata</i> (Busk, 1852)	77, 111, 127, 129, 137, 140, 146, PR
<i>Diphasia digitalis</i> (Busk, 1852)	136
<i>Dynamena quadridentata</i> Ellis & Solander, 1786	87
<i>Dynamena bilamellata</i> sp. nov.	87
<i>Dynamena mertonii</i> (Stechow and Müller, 1923)	147, 52, 156, 40, 160, PD, PR
<i>Tridentata</i> sp.	156
<i>Idiellana pristis</i> (Lamouroux, 1816)	7, 13, 20, 26, 27, 35, 36, 40, 48, 50, 53, 57, 58, 74, 78, 80, 81, 82, 84, 85, 88, 97, 121, 122, 127, 129, 132, 136, 137, 140, 146, 147, 148, 150, 154, 159, 161, PD, PR, EP
<i>Idiellana lepida</i> sp. nov.	PR
<i>Salacia hexodon</i> (Busk, 1852)	7, 20, 42, 54, 89, PR
<i>Salacia sinuosa</i> (Bale, 1884)	48, 100, 137, 139, 147, 154, 155, 156
<i>Salacia tetracythara</i> (Lamouroux, 1816)	81, 126, 152, 155
<i>Salacia flavidula</i> sp. nov.	PR
<i>Salacia alata</i> sp. nov.	40
<i>Salacia bidentata</i> sp. nov.	132
<i>Sertularella decipiens</i> Billard, 1919	40, 147, 153, 154
<i>Sertularella quadridens</i> (Bale, 1884)	97, 138 EP, PR
<i>Sertularella diaphana</i> (Allman, 1885)	40, 87, 110, 113, 131, 146, 154, 156, EP, PR
<i>Sertularia trigonostoma</i> Busk, 1852	7, 82, 84, 138, 154
<i>Thuiaria operculata</i> sp. nov.	146, EA
<i>Thuiaria plumularioides</i> sp. nov.	110, 153, 154
<i>Thyroscyphus macrocytharus</i> (Lamouroux, 1824)	154
<i>Thyroscyphus torresii</i> (Busk, 1852)	13, 48, 67, 78, 87, 110, 127, 136, 137, 138, 155, EA, PD, PR
<i>Thyroscyphus fruticosus</i> (Esper, 1793)	PD, PR
<i>Syntheicum campylocarpum</i> Allman, 1888	13, 20, 21, 26, 81, 110, 111, 26, EA, PR
<i>Syntheicum orthogonium</i> (Busk, 1852)	7, 20, 40, 87, 126, 136, PR
<i>Antennella secundaria</i> (Gmelin, 1791)	7, 37, 82, 84, 95, 110, 111, 127, 136
<i>Halopteris polymorpha</i> (Billard, 1913)	129, 146, 138, EP
<i>Halopteris plagiocampa</i> (Pictet, 1893)	121
<i>Monothecha flexuosa</i> (Bale, 1894)	87
<i>Nemertesia cylindrica</i> (Kirchenpauer, 1876)	121, 136, 139, 146, 147, 91, 137, EA, PR
<i>Plumularia badia</i> Kirchenpauer, 1876	52, 58, 67, 95, 101 EA, EP, PR
<i>Plumularia scabra</i> Lamarck, 1816	80, 136, 137, 147, PR
<i>Plumularia setacea</i> (Linnaeus, 1758)	40, 137
<i>Plumularia bedoti</i> (Billard, 1911)	136
<i>Plumularia tubacarpa</i> sp. nov.	87
<i>Polypumularia cornuta</i> (Bale, 1884)	66, 67, 92, 87, EA
<i>Kirchenpaueria irregularis</i> Millard, 1958	PD
<i>Aglaophenia delicatula</i> (Busk, 1852)	40, 81, 127, 153, 154, 156, PR
<i>Gymnangium hians</i> (Busk, 1852)	154, EP, PR
<i>Gymnangium longicorne</i> (Busk, 1852)	7, 40, 32, 38, 77, 78, 81, 87, 91, 97, 104, 110, 127, 129, 136, 137, 144, 147, 149, 150, 152, 156, 157, 159, 160, EA, PR
<i>Gymnangium undulatum</i> sp. nov.	PR
<i>Gymnangium uninense</i> sp. nov.	77, 104, 110,
<i>Lytocarpia angulosa</i> (Lamarck, 1816)	17, 27, 67, 77, 82, 87, 89, 93, 100, 104, 105, 110, 111, 113, 114, 115, 116, 119, 120, 126, 127, 132, 136, 161, EA
<i>Lytocarpia phyteuma</i> (Kirchenpauer, 1872)	154, EP
<i>Macrorhynchia philippina</i> (Kirchenpauer, 1872)	49, 61, 110, 127, PD, EP
<i>Macrorhynchia phoenicia</i> (Busk, 1852)	7, 127, 137, 136, 138, 154, 156, EA, PR
<i>Macrorhynchia ambigua</i> sp. nov.	PD, PR
<i>Macrorhynchia quadriarmata</i> sp. nov.	137
<i>Clytia ?warreni</i> Stechow, 1919	87
<i>Clytia linearis</i> (Thornely, 1900)	56
<i>Clytia</i> sp. 1	61
<i>Clytia</i> sp. 2	38

SYSTEMATIC REPORT

Order Conica Broch, 1910

Family Campanulinidae Hincks, 1868

Genus *Lafoeina* G.O. Sars, 1874*Lafoeina amirantensis* (Millard and Bouillon, 1973)

(Fig. 2A, B)

Egmundella amirantensis Millard and Bouillon, 1973: 40. - Millard 1975: 133. - Gibbons and Ryland 1989: 389. - Ramil and Vervoort 1992: 22.

Lafoeina amirantensis - Calder 1991: 10. - Watson 1994: 147. - Calder and Vervoort 1998: 15.

Records and material. NTM C12947, alcohol preserved material; NTM C12607, microslide, from infertile colony, Stn 38. NTM C12608, microslide, from infertile colony from Stn 146. Both colonies on calcareous bryozoan.

Description. Colonies stolonial, hydrothecae minute, arising at intervals from a creeping tubular hydrorhiza. Hydrothecae tubular, perisarc thin, sometimes asymmetrically curved, base expanding from a very short pedicel, body of hydrotheca increasing slightly in diameter just below margin. Operculum of many fine segments loosely overlapping at apex; no line of demarcation between opercular segments and hydrothecal body. Nematotheca clavate, very small, borne on stolon between hydrothecae.

Colour. Colourless to white.

Measurements (μm).

Hydrotheca	
length including operculum	120 - 200
maximum width	52 - 72

Nematotheca	
length	32 - 36

Remarks. The specimen and the single nematotheca in the sample conform to previous descriptions and dimensions of *L. amirantensis* (Watson 1994).

Distribution. Indian Ocean (Millard and Bouillon 1973), Mediterranean Sea, east Atlantic (Ramil and Vervoort 1992), Bermuda (Calder 1991), Fiji (Gibbons and Ryland 1989), and mid-Atlantic Ridge (Calder and Vervoort 1998). This is the second Australian record of *L. amirantensis*, the first being from Bass Strait, southern Australia (Watson 1994).

Family Lafoeidae A. Agassiz, 1865

Genus *Filellum* Hincks, 1868*Filellum ?serratum* (Clarke, 1879)

(Fig. 2C)

Lafoea serrata Clarke, 1879: 242. - Hartlaub 1905: 595.

Reticularia serrata - Ralph 1958: 312.

Filellum serratum - Millard 1975: 178. - Gravier-Bonnet 1979: 22. - Ramil and Vervoort 1992: 54. - Hirohito 1995: 110. - Peña Cantero *et al.* 1998: 304.

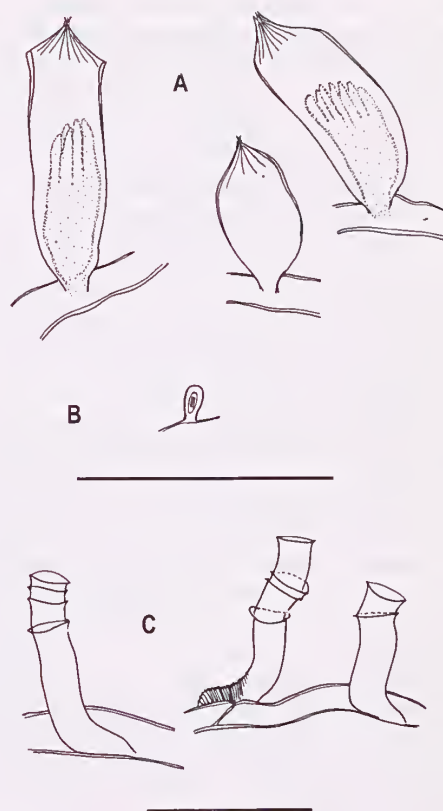


Fig. 2. A, B. *Lafoeina amirantensis*: A, hydrothecae. B, nematotheca. C, *Filellum ?serratum* on *Idliellana pristis*. Scale bars: A, B, 200 μm ; C, 500 μm .

Records and material. NTM C12609, microslide, sparse infertile colony creeping on *Idliellana pristis*, Stn 121. *Other record.* Plater Rock, infertile colony on aglaopheniid stem, coll: J. E. Watson, depth 10 m, 21/9/1999.

Description. Hydrothecae erect, long, tubiform, narrowing proximally to junction with hydrorhiza; marginal rim slightly but distinctly everted, marginal replications common. Anterior adnate surface closely transversely striated in some hydrothecae, smooth in others.

Colour. Colourless.

Measurements (μm).

Hydrotheca	
length of free part	320 - 560
diameter at margin	96 - 128

Remarks. In the absence of a coppinia it is difficult to distinguish between *Filellum antarcticum* and *Filellum serratum*, especially when proximal striations are variable among hydrothecae as in the present material. Striations typical of *F. serratum* are also reported to occur on some hydrothecae of *F. antarcticum* (Millard 1975). The present material is therefore

doubtfully assigned to *F. serratum* on the basis of the longer erect part of the hydrothecae and shorter adnate part, more typical of *F. serratum* than *F. antarcticum*.

Distribution. Cosmopolitan (Peña Cantero *et al.*, 1998). Previously recorded from Western Australia (Stechow 1925, Watson 1996).

Genus *Hebellopsis* Hadzi, 1913

***Hebellopsis costata* (Bale, 1884)**

(Fig. 3A)

Campanularia costata Bale, 1884: 56. - Stechow and Müller 1923: 463.

Scandia corrugata Millard and Bouillon, 1973: 60.

Hebella muscensis Millard and Bouillon, 1975: 10. - Boero *et al.* 1997: 22.

Records and material. NTM C12941, alcohol preserved material; NTM C12610, MV F86888, microslides, colony on *Idiellana pristis* from Stn 57. NTM C12943, alcohol preserved material from Stn 13. NTM C12942, alcohol preserved material from Stn 85. *Other records.* Many infertile colonies on *Thyroscyphus torresi*, *Syntheicum campylocarpum* and aglaopheniid hydroids, Stns 7, 8, 13, 38, 40, 53, 80, 136, 137, 140, 146, 159. Wharf pilings, Port of Darwin, infertile colonies on other hydroids, coll: J. E. Watson, depth 1 - 10 m, 16/9/1998. Plater Rock, infertile colonies on aglaopheniids and *Idiellana pristis*, coll: J. E. Watson, depth 4 - 10 m, 19/9/1999. East Point, infertile colonies on *Thyroscyphus torresii*, coll: J. E. Watson, depth 1 m, 19/9/1999.

Description. Hydrorhiza tubular, creeping on stems and branches of host. Hydrothecal pedicel short, tubular, perisarc smooth, widening a little distally and merging into base of hydrotheca. Hydrotheca long, tubular, perisarc thick, inclined to one side in distal third so that one wall convex and other concave, body with 8 - 11 deep entire annulations these becoming indistinct proximally, in some hydrothecae annulations reduced to undulations. Margin circular, with up to four replications, inclined to hydrothecal axis, rim distinctly everted, perisarc fairly thin. Diaphragm saucer-shaped, thin, indistinct, without thickening along hydrothecal wall, in empty hydrothecae line of attachment of hydranth marked by a row of internal upward-facing, thorn-like desmocytes. Hydranths too poorly preserved for tentacle count.

Colour. White to colourless.

Measurements (µm).

Pedicel	
length	136 - 160
diameter below hydrotheca	96 - 136
Hydrotheca	
length, diaphragm to margin, convex wall	1,000 - 1,120
diameter of margin, including everted rim	440 - 500
width of marginal rim	48 - 56

Remarks. The specimens conform exactly with Bale's (1884) description and figures of *Hebellopsis costata* epizootic on *Idiellana pristis* from the type locality of Port Darwin. Dimensions of the hydrothecal arc, however, a little greater than those extracted from Bale's figure. No gonothecae were found among the abundant material in the collection.

Millard and Bouillon (1975) were unable to distinguish between sterile colonies of *Scandia corrugata* and *Hebella costata*, and regarded both as *nomina oblita*, replacing the name *H. costata* with *H. muscensis* and *S. corrugata* with *S. tubitheca*. Their opinion, adopted by Boero *et al.* (1997) is untenable since both *H. costata* and *H. corrugata* are valid names used in the literature during the past 50 years (Billard 1941, Pennycuik 1959, Mammen 1965 and see Calder 1991).

Distribution. Indian Ocean, (Millard and Bouillon 1975) Papua New Guinea (Boero *et al.* 1997), Australia (Bale 1884).

***Hebellopsis scandens* (Bale, 1888)**

(Fig. 3B, C)

Lafaea scandens Bale, 1888: 758. - Jäderholm 1903: 274; - Billard 1904: 481; - Billard 1906: 174; - Warren 1908: 272, 341, 349.

Hebella scandens - Marktanner-Turneretscher 1890: 214. - Millard 1975: 182. - Gili and Ballesteros 1991: 247. - Genzano 1992: 144. - Migotto 1996: 26. - Watson 1996: 78. - Migotto 1997: 35. - Boero *et al.* 1997: 8.

Hebellopsis scandens - Vannucci 1949: 237. - Vannucci 1950: 85. - Calder 1991: 43, 45, 95.

Records and material. NTM C13082, MV F86890, microslides, infertile colonies on *Syntheicum campylocarpum* from Stn 20. *Other records.* Port of Darwin on wharf pilings, fertile colonies on *Idiellana pristis* and *Thyroscyphus torresi*, coll: J. E. Watson, depth 1-10 m, 18/9/1998. Plater Rock, infertile colony on aglaopheniid stem, coll: J. E. Watson, depth 10 m, 21/9/1999.

Description. Hydrorhiza reptant on host; hydrothecae long, tubular, directed upwards for first third or half of length then bending sharply outwards and often downwards, lower wall with a deep inflexure but without internal thickening of perisarc; perisarc moderately thick, thinning to margin. Margin transverse, circular, even, with a short outrolled rim; some margins replicated two or three times

Colour. Transparent white.

Measurements (µm).

Hydrorhiza, diameter	64
Hydrotheca	
length abcauline wall, base to bend	224 - 296
length abcauline wall, bend to margin	200 - 304
diameter at margin	144 - 192

Genus *Hebella* Allman, 1888
***Hebella* ?*laterocaudata* Billard, 1942**
 (Fig. 3D)

Hebella laterocaudata Billard, 1942: 69. - Van Praët 1979: 883. - Van Soest 1976: 81. - Boero 1980: 134. - Calder 1991: 39. - Boero *et al.* 1997: 18.

Record and material. NTM C12612, small infertile colony on stem of *Idiellana pristis* from Stn 139.

Description. Hydrorhiza very thin, tubular, reptant on branches of host, following imbrications of adnate hydrothecal walls of host. Hydrothecae emergent between *Idiellana* hydrothecae, proximal wall of *Hebellopsis* resting on adcauline wall of host; hydrotheca tubiform, asymmetrical, usually inclined downwards, sometimes projecting directly away from host, wall in contact with host convex, free wall sinuous, swollen proximally, floor rounded, hydropore inserted on abcauline side of floor. Marginal rim circular, transverse, very thin, neither everted nor replicated.

Colour. White to colourless.

Measurements (µm).

Diameter of hydrorhiza	52
Hydrotheca	
length	280 - 320
diameter at margin	120 - 128

Remarks. The hydrorhiza appears to be too weak to support the hydrothecae, so that most rest on the adcauline hydrothecal walls of the host. The short, stubby hydrotheca with eccentrically placed hydropore is closest to *Hebella laterocaudata*; the hydrotheca is, however, shorter than the length of 560 µm given by Van Praët for that species, the hydrotheca narrows, rather than expands distally and the pedicel is smooth rather than slightly undulated as in Billard's (1942) figure. As the material consists of only one small, infertile colony, it is assigned with some reservation to *H. laterocaudata*.

Distribution. Indonesia (Billard 1942). This is the first record of the species from the Australian region.

**Genus *Anthohebella* Boero, Bouillon
and Kubota, 1997**

Boero *et al.* (1997) proposed the genus *Anthohebella* to accommodate hebellid species showing general characters of the subfamily Hebellinae but liberating swimming gonophores rather than a medusa. A hebellid species collected in Darwin Harbour, which generally conforms with these authors' concept of *Anthohebella*, but which liberates a partially formed medusa necessitates amendment of the generic diagnosis of *Anthohebella*.

Amended diagnosis of *Anthohebella*. Colony stolonial, hydrotheca borne on a short pedicel, campanulate or cylindrical, usually with annular thickening and thin membranous diaphragm. Hydranth with conical hypostome. Gonotheca solitary, originating from hydrorhiza, with or without opercular flaps. Swimming

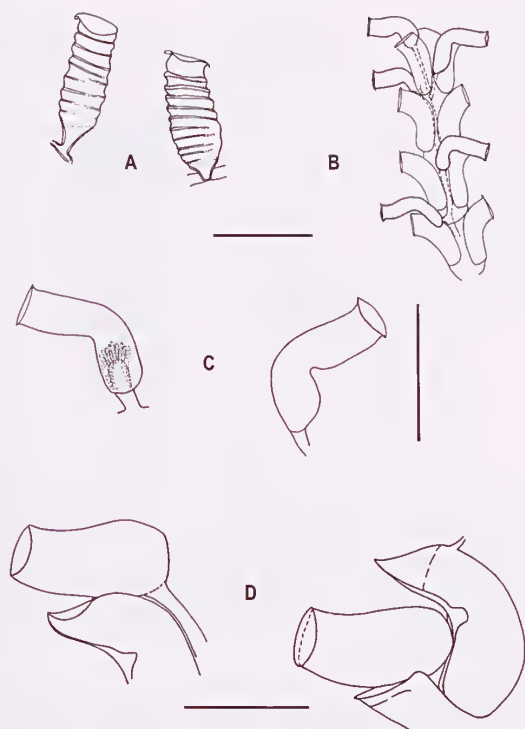


Fig. 3. A. *Hebellopsis costata*: two hydrothecae from colony on *Idiellana pristis*. B, C, *Hebellopsis scandens*: B, colony on *Synthecium campylocarpum*, hydrothecae inserted between those of host. C, strongly flexed hydrotheca with everted margin. D, *Hebella*? *laterocaudata*, infertile colony on *Idiellana pristis*. Scale bars: A, B, 1,000 µm; C, D, 500 µm.

Remarks. Boero *et al.* (1997) reported colonies of *Hebella scandens* from Papua New Guinea the hydrothecae of which ranged in shape from almost straight to a right-angle bend. Hydrothecae from Beagle Gulf also show this morphological range, although it does not occur along the same colony as described by Boero *et al.* Colonies on *Thyroscyphus torresii* from Plater Rock show even more extreme torsion, all hydrothecae having two sharp right-angled bends. Neither singly nor doubly bent hydrothecae on any of the colonies I have examined seem to result from being forced to accommodate to the morphology of the host hydrothecae as described by Boero *et al.*, most, especially those on *T. torresii* being freely reptant. Either *H. scandens* shows extreme morphological variation according to the host species or there may be a different, although closely related species involved. The question must remain unresolved until fertile material of the doubly bent form is found.

Distribution. Cosmopolitan. Type locality, south-eastern Australia (Bale 1888).

gonophore with or without a velum, four radial canals, four marginal reduced tentacles or atentaculate bulbs, and gametes on the spadix.

***Anthohebella parasitica* (Ciamician, 1880)**
(Fig. 4A, B)

Lafaea parasitica Ciamician, 1880: 673.

Hebella parasitica - Marktanner-Turneretscher 1890: 213. - Hadzi 1913: 105. - Leloup 1937: 4, 28. - Leloup 1938: 8. - Da Cunha 1950: 124. - Rossi 1950: 25. - Dawydoff 1952: 55. - Picard 1952: 347. - Yamada 1958: 51, 55. - Yamada 1959: 45. - Riedl 1970: 150. - Vervoort and Vasseur 1977: 12. - Mergner and Wedler 1977: 16. - Boero 1980: 142. - García *et al.* 1979: 16. - Gili 1982: 71. - Boero and Fresi 1985: 143. - Gili and Castelló 1985: 13. - Boero and Bouillon 1989: 37. - Gibbons and Ryland 1989: 380, 394. - Ryland and Gibbons 1991: 527, 559. - Hirohito 1995: 122. - Watson 1996: 78.

Anthohebella parasitica - Boero *et al.* 1997: 24.

Records and material. NTM C12613, MV F86891 microslides from Stn 7. NTM C12614, microslide, from Stn 33. *Other records.* Stns 13, 38, 40, 53, 137, 146, 159, many infertile colonies on stems of *Gymnangium longicorne*. Plater Rock, infertile colonies on stems of aglaopheniid hydroid, coll: J. E. Watson, depth 10 m, 22/9/1999.

Description. Hydorrhiza tubular, creeping on stem of *Gymnangium longicorne*, stolons running parallel along fascicular tubes of host. Hydrothecal pedicels long, deeply and roughly corrugated, perisarc very thick, merging into body of hydrotheca.

Hydrotheca large, deeply campanulate, asymmetrical, lower third of one wall convex, body then becoming almost tubiform, walls smooth to slightly undulated, perisarc moderately thick, thinning towards margin. Diaphragm shallow dish-shaped, indistinct, marked by a granular thickening at base of hydrotheca. Margin oblique with a large, strongly outrolled rim, perisarc of rim thin, some margins with a single replication. Hydranths large, not well preserved, with c. 25 tentacles.

Measurements (µm).

Pedicel

length to diaphragm	400 - 720
diameter at junction with hydorrhiza	104 - 144

Hydrotheca

length, diaphragm to margin	1,000 - 1,160
diameter at diaphragm	220 - 300
diameter at margin	66 - 800
width of marginal flange	96 - 112

Remarks. *Anthohebella parasitica* was abundant on stems of many of the larger aglaopheniid hydroids from many localities.

Distribution. Widely distributed in tropical and subtropical Pacific and Atlantic Oceans (Vervoort and Vasseur 1977), Mediterranean Sea (Boero 1980),

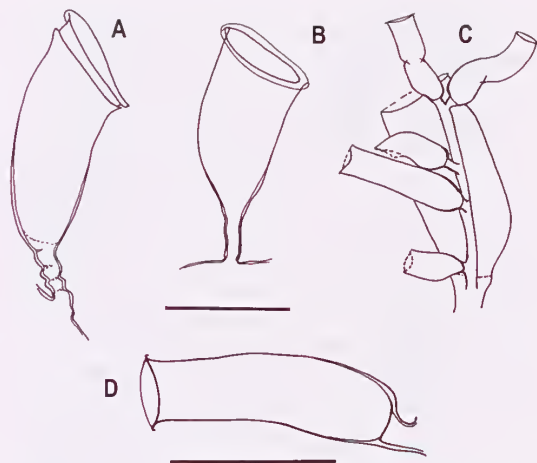


Fig. 4. A, B, *Anthohebella parasitica* from stem of *Gymnangium longicorne*: A, hydrotheca with replicated margin and undulated pedicel. B, hydrotheca with smooth pedicel. C, D, *Hebellopsis hartmeyeri* Stechow and Müller, 1923 drawn from type specimen on *Lytoscyphus fruticosus*: C, part of colony. D, hydrotheca showing diaphragm and strongly outrolled marginal rim. Scale bars: A, B, C, 1,000 µm; D, 500 µm.

doubtfully recorded from Japan (Hirohito 1995). Recorded from Western Australia (Watson 1996).

***Anthohebella darwineensis* sp. nov.**
(Fig. 5A-D)

Record and material. Holotype, NTM C12958, alcohol preserved material; NTM C12615, NTM C12616, MV F86889, microslides from holotype, fertile colony on *Thyrosocyphus torresi*, from bed of channel, East Arm port site, Darwin Harbour depth 6 m, coll: J. E. Watson 17/8/1998.

Description. Colony stolonal, hydorrhiza tubular, reptant on stem and branches of host. Hydrotheca arising from stolon at regular intervals, usually beside a hydrotheca of host. Hydrotheca long, narrow, tubiform, bending outwards from hydorrhiza and away from host; pedicel short, asymmetrically placed at base of hydrotheca, sometimes with a single twist. Diaphragm thin, concave, adjoined to wall by a ring of perisarc, better developed as a triangular shelf on adcauline wall. Margin circular, not everted, sometimes with a single replication; perisarc of hydrotheca moderately thick. Hydranth with conical hypostome surrounded by 20 - 24 tentacles.

Gonotheca large, elongate conical, borne without pedicel on hydorrhiza, orifice distal, circular, operculum a single flap, perisarc of gonotheca thin. Nearly mature gonophore a single large eumedusoid; umbrella a small disk with four vestigial radial canals; four long rudimentary tentacles contracted into a wavy pattern; no velum or manubrium.

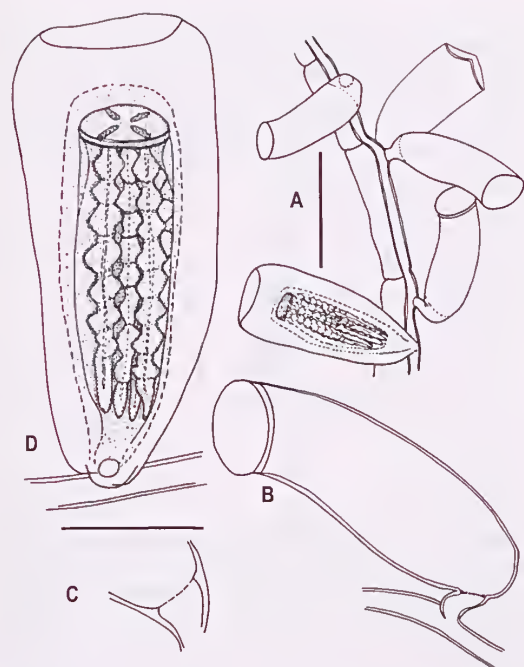


Fig. 5. *Anthohebella darwinensis* sp. nov. A, part of fertile holotype colony on *Thyroscyphus torresii*. B, hydrotheca, showing replicated margin. C, base of hydrotheca showing thin diaphragm and perisarc. D, gonotheca with nearly mature cumedusoid. Scale bars: A, 1,000 μ m; B - D, 500 μ m.

Colour. In life, hydrotheca white, gonotheca transparent to bluish-white, tentacles of gonophore white to pink, radial canals pink.

Measurements (μ m).

Hydrotheca

length of pedicel (to diaphragm)	160 - 200
narrowest width of pedicel	300 - 360
length, margin to diaphragm	960 - 1,360
diameter at margin	368 - 424

Gonotheca

length	1,600 - 1,760
maximum width	700 - 740

Remarks. The decidedly asymmetrical position of the hydrothecal pedicel permits bending of the hydrotheca alongside the hydrotheca of the host but depending on aspect of view, the pedicel may appear to be centrally placed. The large, solitary cumedusoids in the sample are almost mature. The umbrella is quite small in comparison with the length of the rudimentary tentacles. Neither manubrium, velum nor gametes were found.

Since the hydrotheca of *Anthohebella darwinensis* resembled figures of *Hebellopsis hartmeyeri* Stechow and Müller, 1923 from the Aru Sea (see Stechow and Müller, 1923, fig. 4), I examined type material of *H. hartmeyeri* loaned by the Zoologische Staatssammlung, Munich, Germany. The type series comprises two

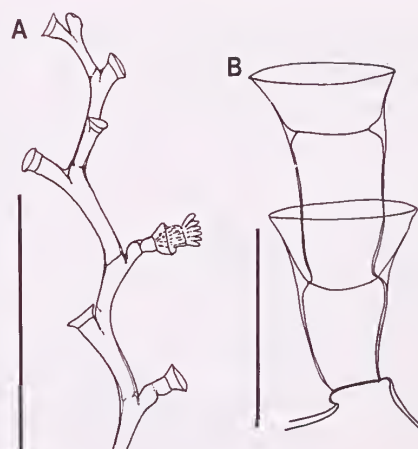


Fig. 6. *Halecium dyssymetrum* from stem of *Gymnangium longicorne*: A, stem. B, primary and secondary hydrophores. Scale bars: A, 2,000 μ m; B, 300 μ m.

microslide preparations containing several hydrothecae but no gonothecae. Both microslides are labelled "*Hebellopsis hartmeyeri*, sp. nov., auf *Lytoscyphus fruticosus*, Aru Inseln, Merton". Stechow and Müller's figure of *H. hartmeyeri* is somewhat misleading as it does not show the everted and outrolled marginal rim distinctly visible in the few undamaged hydrothecae in the microslides. Although considerably larger, the hydrotheca of *H. hartmeyeri* closely resembles *Hebella scandens* Balch. For comparison with *A. darwinensis*, *Hebellopsis hartmeyeri* is drawn from the type microslide (Fig. 4C-D).

Etymology. Named for the type locality of Darwin Harbour.

Family Haleciidae Hincks, 1868

Genus *Halecium* Oken, 1815

***Halecium dyssymetrum* Billard, 1929**
(Fig. 6A-B)

Halecium dyssymetrum Billard, 1929: 307. - Leloup 1935: 1. - Millard 1975: 150. - Watson 1996: 78. - Migotto 1996: 32. - Watson 1997: 514.

Endothecium dyssymetrum - Calder 1991: 15.

Records and material. NTM C12921, alcohol preserved material; NTM C12617, microslide, infertile colony on *Gymnangium longicorne* from Stn 40. *Other records.* East Point, many infertile colonies on coral rubble, coll: J. E. Watson, depth 1 m, 26/9/1999.

Description. Hydorhiza tubular, reptant on host; stems to 5 mm high, simple, monosiphonic, internodes geniculate, nodes oblique, indistinct to absent. Primary hydrophore distal on stem internode, long, expanding to diaphragm; diaphragm marked by an internal flexure of perisarc, secondary hydrophores when present, arising from diaphragm of primary hydrotheca. Hydrotheca deep

bowl-shaped, expanding to a circular margin; margin not everted. Hydranths large.

Colour. White.

Measurements (μm).

Stem

length of internode	400 - 600
diameter at node	112 - 152

Hydrotheca

length of primary hydrophore to diaphragm	60 - 360
depth of hydrotheca, diaphragm to margin	100 - 180
diameter at diaphragm	120 - 160
diameter of margin	200 - 236

Remarks. The species conforms to the description and dimensions of *Halecium dyssymetrum* reported from Western Australia (Watson 1997). Abundant infertile colonies were found on coral rubble in shallow water at East Point (author's observation, Sept. 1999).

Distribution. *Halecium dyssymetrum* is known from the Indian Ocean, Indo-Pacific and West Indies (Millard 1975). Australian distribution: Houtman Abrolhos Islands, Western Australia (Watson 1997).

Halecium spatulum sp. nov.
(Fig. 7A-E)

Halecium beanii (Johnston, 1838). - Stechow and Müller 1923: 460.

Records and material. Holotype, NTM C13049, alcohol preserved material, NTM C12618, NTM C12619, microslides from holotype, female colony on *Eunice tubifex*, Port of Darwin, on wharf pilings, coll: J. E. Watson, depth 8 m, 18/9/1998. Paratypes, NTM C12620, microslide, colony detached from substrate, Stn 40. NTM C12623, microslide, sparingly fertile colony creeping on aglaopheniid stem, Stn 48. *Other records.* Plater Rock, infertile colonies on other invertebrates, coll: J. E. Watson, depth 5-10 m, 22/9/1999.

Description. Hydrorhiza reptant on substrate, stems to 10 mm high, lower stems lightly to heavily fascicled, irregularly branched in one to several orders of branching more or less in the same plane; branches given off opposite stem node, stem and branch internodes long, straight, smooth, expanding distally to hydrophore, nodes oblique, facing in opposite directions, a tumescence above and below node. Primary hydrophores alternate, short, usually a minute saddle-shaped notch between hydrophore and stem, secondary hydrophores common, tertiary hydrophores rare; secondary hydrophores variable in length, base tumid on adcauline side, walls expanding evenly to margin. Hydrotheca shallow dish-shaped, expanding a little to a circular margin with thin, not everted rim; some hydrothecal margins replicated one or twice, diaphragm distinct, a few very small ellipsoidal desmocytes above diaphragm.

Hydranths extensible, with c. 16 tentacles.

Gonotheca elongated, spatulate, widening from base to distal margin, arising without distinct pedicel from below a primary hydrophore, distal end truncate, slightly domed, no operculum, perisarc thin and smooth.

Colour. Fascicled stems pale brown, becoming white in monosiphonic parts, female gonophore pale blue.

Measurements (μm).

Stem and branches

length of internode	400 - 504
width at node	64 - 80

Hydrotheca

primary hydrophore, depth margin to diaphragm	24 - 28
diameter at margin	88 - 120
secondary hydrophore, depth, base to margin	120 - 208

Gonotheca

maximum length	440 - 460
distal width	136 - 200

Remarks. Material of *Halecium spatulum* from Beagle Gulf is meagre in comparison to the abundant colonies collected in the environs of Darwin. The fragile, lacy, white colonies are easily recognised *in situ*. The few gonothecae present in the Beagle Gulf collection were empty; those from Darwin Harbour were mature female, each gonophore containing many small ova.

In size and shape of colony *Halecium spatulum* resembles *H. lankesteri* (Bourne, 1890); however, the marginal rim of the hydrotheca is more flaring in that species (see Cornelius 1995). *Halecium spatulum* is also closely related to *H. sibogae* Billard, 1929 (see Gibbons and Ryland 1989, Ramil and Vervoort 1992), but lacks the comma-shaped notch at the base of the adcauline hydrothecal wall found in that species. Furthermore, the marginal rim is much less everted than shown by Ramil and Vervoort (1992), for *H. sibogae marconanum* Billard, 1934. An infertile specimen referred to *H. beanii* (Johnston, 1838) by Stechow and Müller (1923) from Aru Island is undoubtedly *H. spatulum*.

Etymology. Named for the spatulate gonotheca.

Genus *Hydrodendrou* Hincks, 1874

Hydrodendrou dichotomum (Allman, 1888)

(Fig. 8A-B)

Diplocyathus dichotomus Allman, 1888: 17. - Kirkpatrick 1890: 604. - Billard 1929: 71. - Leloup 1939: 5. - Yamada 1959: 35.

Ophiodes dichotomus - Billard 1910: 4. - Jäderholm 1916: 4.

Hydrodendron dichotomus - Pennycuik 1959: 155. - Hirohito 1983: 13.

Hydrodendron dichotomum - Rees and Vervoort 1987: 14. - Watson 1996: 78.

Records and material. NTM C12922, alcohol preserved material; NTM C12621, NTM C12622, MV F86894, microslides, large infertile colony intergrown

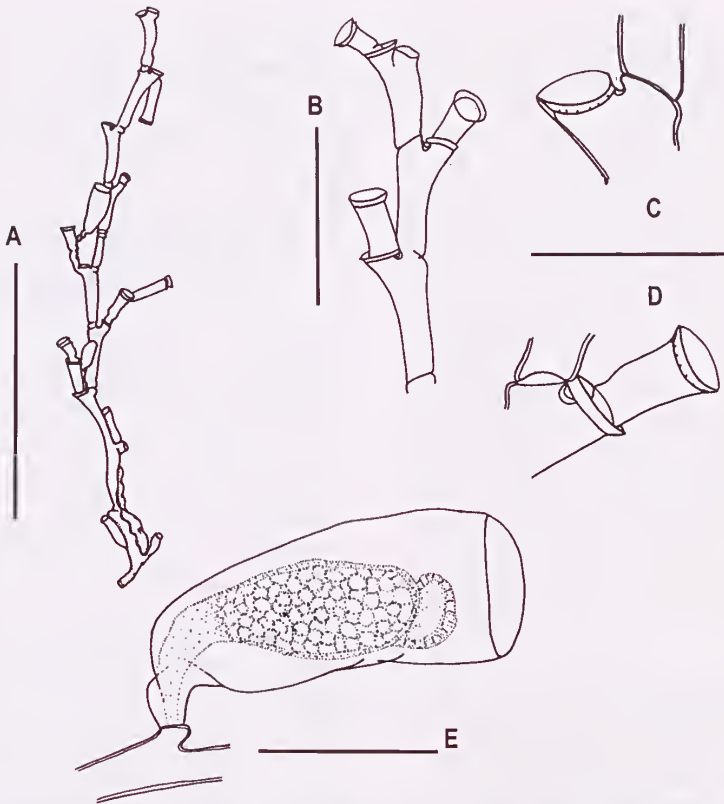


Fig. 7. *Halecium spatulum* sp. nov. A, stem from holotype colony. B, stem internodes from holotype. C, D, primary and secondary hydrophores from holotype. E, female gonotheca from paratype NTM C12623. Scale bars: A, 2,000 μ m; B - D, 300 μ m; E, 500 μ m.

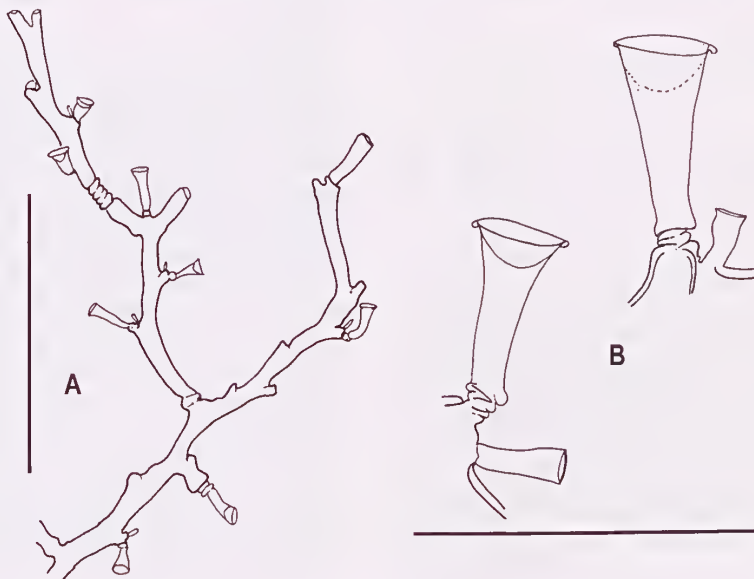


Fig. 8. *Hydrodendron dichotomum*: A, stem. B, hydrothecae with strongly outrolled marginal rim and short and long dactylothecae. Scale bars: A, 2,000 μ m; B, 500 μ m.

with bryozoan, from Stn 138. NTM C12923, MV F86947, alcohol preserved material; NTM C13078, microslide, infertile colony from wharf pilings, Port of Darwin, coll: J. E. Watson, depth 12 m, 16/8/1998. *Other records.* Plater Rock, infertile colony on sponge, coll: J. E. Watson, depth 10 m, 21/9/1999.

Description. Colonies to 70 x 70 mm, hydrocaulus unfascicled, a tangled and anastomosing mass of dichotomous branches without main stem. Branches and hydrorhiza of same diameter; cauline perisarc very thick proximally, thinning a little toward distal end of branches. Branches usually given off from distal part of internode below an oblique to transverse node; in younger branches sometimes an extra node or a series of imperfect internodal annulations, a hydrophore in each branch dichotomy. Hydrophores alternate on younger branches, borne distally on internode on short, thickened apophyses, pedicel crumpled, walls of hydrophore above pedicel swollen, more tumid on adcauline side, walls thereafter smooth, expanding evenly to hydrothecal margin; diaphragm deep bowl-shaped, no desmocytes observed; margin circular, rim everted and somewhat outrolled.

Nematothecae borne on a small platform below apophysis, vase-shaped to almost tubiform, narrowest at base and slightly constricted just below margin, rim circular, sometimes weakly everted, perisarc thin.

Hydranths extensible, with c. 30 tentacles.

Colour. Live colony pale yellow-brown, hydrothecae white.

Measurements (µm).

Stem	
length of internode	400 - 440
diameter of internode	
above apophysis	152 - 184
Hydrotheca	
length	256 - 352
diameter at base	40 - 56
diameter at margin	136 - 160
Nematotheca	
length	80 - 120
diameter at margin	40 - 60

Remarks. The colonies are so intimately intergrown with their invertebrate substrates that it is difficult to disentangle them. Few hydrothecae and axillary nematothecae remain on older branches. No secondary hydrothecae or desmocytes were seen in the samples.

The material corresponds to the description and figures of *Hydrodendron dichotomum* from Cape York, northern Australia (Allman 1888) and Indo-Pacific localities given by other authors. The hydrothecae and nematothecae are somewhat larger than dimensions given by Rees and Vervoort (1987) for material from the Gulf of Aden. *Hydrodendron dichotomum* is an epizooite of invertebrates in Darwin Harbour; it has also been

reported on sponge and antipatharians by Rees and Vervoort (1987).

Distribution. Indo-West Pacific, Gulf of Aden (Rees and Vervoort 1987). Type locality, Torres Strait (Allman 1888); also recorded from tropical eastern and western Australia (Pennycuik, 1959, Watson 1996) and Timor Sea.

Family Sertulariidae Lamouroux, 1812

Genus *Diphasia* L. Agassiz, 1862

Diphasia mutulata (Busk, 1852)

(Fig. 9A-G)

Sertularia mutulata Busk, 1852: 391.

Diphasia mutulata - Bale 1884: 101. - Ritchie 1910: 12. - Thornely 1904: 118. - Thornely 1908: 83. - Billard 1933: 16. - Mergner and Wedler 1977: 18. - Watson 1996: 78.

Diphasia pinaster Billard, 1907: 357.

Diphasia heurteli Billard, 1924: 67. - Millard 1975: 258.

Diphasia heurteli var. *simplex* Billard, 1933: 19.

Nigellastrum mutulatum - Stechow and Müller 1923: 468.

Records and material. NTM C12907, alcohol preserved material; NTM C12624, NTM C12626, MV F86908, microslides, colonies on stems of agalopheniids, bryozoans and *Idiellana pristis* from Stn 77. NTM C12906, alcohol preserved material; NTM C12625, microslides from Stn 146. MV F86907, microslide, colony on *Idiellana pristis* from Stn 111. MV F86937, alcohol preserved material, from Stn 137. *Other records.* Stns 127, 129. Plater Rock, fertile colonies on stems of agalopheniid hydroids, coll: J. E. Watson, depth 9 m, 22/9/1999.

Description. Colonies of simple stems to 10 mm high arising at intervals from tubular hydrorhizae creeping on host; stems unbranched, proximal stem region variable in length, tubular, athecate, perisarc smooth, ending in a strong hinge joint. Hydrothecae biserial, paired, sometimes in contact, one pair on internode, nodes transverse, indistinct or absent.

Two distinct kinds of stems, each with differently shaped hydrothecae morphologically similar to *Diphasia mutulata* and *D. heurteli* occur in the colony.

Diphasia mutulata morph: tubular, adcauline wall sinuous, often a distinct hump in mid-region, free adcauline wall one quarter to one third length of adnate wall; abcauline wall concave to sinuous, deflected outwards, sometimes an internal shelf of perisarc well below margin; margin large, shovel-shaped, facing upwards, operculum dome-shaped, perisarc very delicate, often collapsed into hydrotheca.

Diphasia heurteli morph: tubular, long, narrow at base, expanding a little to margin, adnate adcauline wall convex, free part concave, c. half adcauline wall free; abcauline wall concave, a long upwardly pointed internal

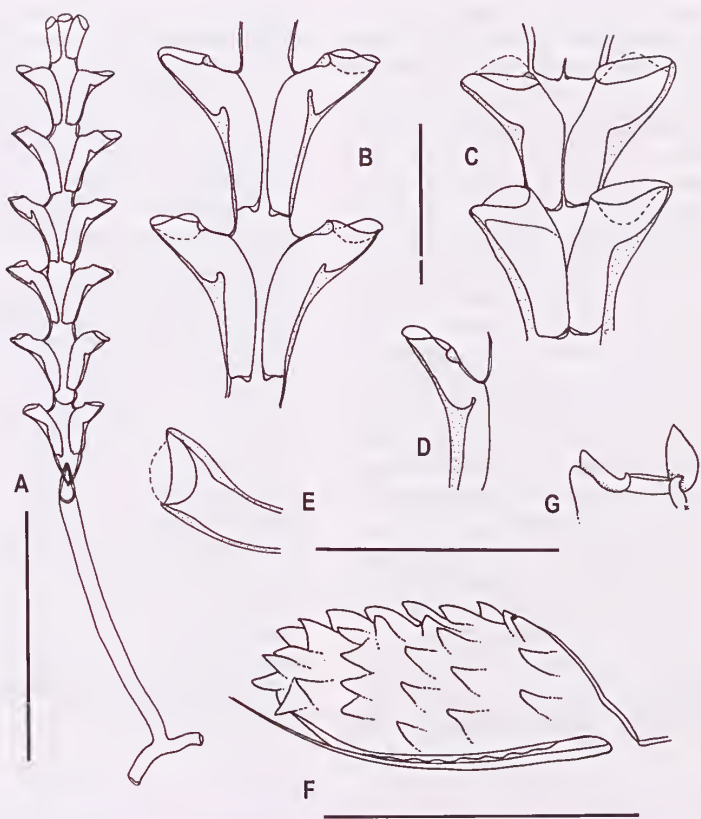


Fig. 9. *Diphasia mutulata*: A, stem from colony on *Idliellana pristis*. B, C, stem internodes from same colony. B, *Diphasia mutulata* morph. C, *Diphasia heurteli* morph. D, lateral view of hydrotheca of *Diphasia mutulata* morph. E, lateral view of hydrotheca of *Diphasia mutulata* morph showing operculum. F, gonotheca. G, orifice of gonotheca with operculum. Scale bars: A, 2,000 µm; B, C, 500 µm; D, E, G, 200 µm; F, 500 µm.

shelf about two-thirds distance up wall; margin facing upwards almost perpendicular to cauline axis with a pair of low lateral lobes, operculum usually collapsed inwards, perisarc delicate.

Gonothecae monoscriate and closely adpressed to hydrocaulus, one between each hydrothecal pair on a short, wide, pedicel; gonotheca ovoid, body covered in irregular rows of short, thick, distally-facing spines, distal orifice a small tube surrounded by spines.

Colour. Pale shining brown.

Measurements (µm).

Stem		
length of athecate part	60	-1,900
diameter of athecate part	88	- 128
Internode		
length of <i>D. mutulata</i> morph	400	- 440
length of <i>D. heurteli</i> morph	408	- 448
width at node, <i>D. mutulata</i> morph	240	- 264
width at node, <i>D. heurteli</i> morph	208	- 240
Hydrotheca		
depth, abcauline margin to base, <i>D. mutulata</i> morph	496	- 520

length adnate adcauline wall, <i>D. mutulata</i> morph	336	- 392
length free adcauline wall, <i>D. mutulata</i> morph	80	- 160
width across pair, margin to margin, <i>D. mutulata</i> morph	720	- 808
width of margin, <i>D. mutulata</i> morph	256	- 280
depth, abcauline margin to base, <i>D. heurteli</i> morph	480	- 504
length adnate adcauline wall, <i>D. heurteli</i> morph	400	- 408
length free adcauline wall, <i>D. heurteli</i> morph	80	- 160
width across pair, margin to margin <i>D. heurteli</i> morph	768	- 808
width of margin <i>D. heurteli</i> morph	176	- 240
Gonotheca		
overall length	584	- 632
width (lateral view)	256	- 272

Remarks. The two morphologically distinct hydrothecae occur on several of the colonies, the most

abundant morph corresponding to *Diphasia mutulata* Busk (1852) and the less abundant to *D. heurteli*. Busk (1852) drew attention to morphological differences between hydrothecae of the stems and branches of *D. mutulata* while Bale (1884) figured three different shapes of hydrothecae for that species. Billard (1907), recorded material from Moçambique as *Diphasia pinaster* (Ellis and Solander 1786) but in 1924 synonymised the name with *D. heurteli*. Millard (1975) remarked upon the similarity of *S. heurteli* and *D. mutulata*, but nevertheless considered the two species separate. In the present material depth of the hydrotheca is similar in both morphs, the main difference between them being the slenderer hydrotheca with a stronger outward bend and much more pronounced internal shelf in the *heurteli* morph (Fig. 9B). The *mutulata* morph is wider across the margins and the margin is broader and more bracket-like (Fig. 9C). There is no discernible intergradation in hydrothecal size or shape between the two morphological extremes in the present colonies and while there is no intermingling, the morphs arise in groups from a common hydrorhiza. The gonotheca of *D. heurteli* figured by Millard (1975) is immature; in the present material gonothecae of both morphs are identical.

Distribution. Torres Strait (Busk 1852), Queensland (Bale 1884) Gulf of Manaar (Thornely 1904), Andaman

Islands (Ritchie 1910), Suez area (Thornely 1908, Billard 1933), Red Sea (Mergner and Wedler 1977).

***Diphasia digitalis* (Busk, 1852)**

(Fig. 10A-B)

Sertularia digitalis Busk, 1852: 387, 393.

Desmoscyphus longitheca Allman, 1877: 26.

Desmoscyphus acanthocarpus Allman, 1888: 73.

Nigellastrum digitale - Stechow 1923: 12, 161.
- Mammen 1965: 57.

Diphasia digitalis - von Lendenfeld 1885a: 415, 633.
- Nutting 1900: 110. Nutting 1904: 110. - Ritchie 1910: 821. - Bale 1884: 101. - Bale 1915: 265. - Jäderholm 1916: 5, 16. - Jäderholm 1916: 16. - Jäderholm 1919: 16. - Jäderholm 1920: 4. - Jarvis 1922: 332, 343. - Hargitt 1924: 501. - Billard 1925: 209. - Gravely 1927: 14. - Nutting 1927: 218. - Billard 1931: 249. - Leloup 1932: 161. - Vervoort 1946: 307. - Vervoort 1959: 254. - Vervoort 1968: 37. - Vervoort 1972: 99. - Dcevey 1954: 270. - Pennycuik 1959: 191. - Yamada 1959: 54. - Rees and Thursfield 1965: 120. - Millard and Bouillon 1973: 67. - Millard and Bouillon 1974: 31. - Millard 1975: 257. - Mergner and Wedler 1977: 16. - Mayal 1983: 7. - Watson 1996: 78.

Record and material. NTM C12627, colony of four small infertile stems on *Idiellana pristin* from Stn 136.

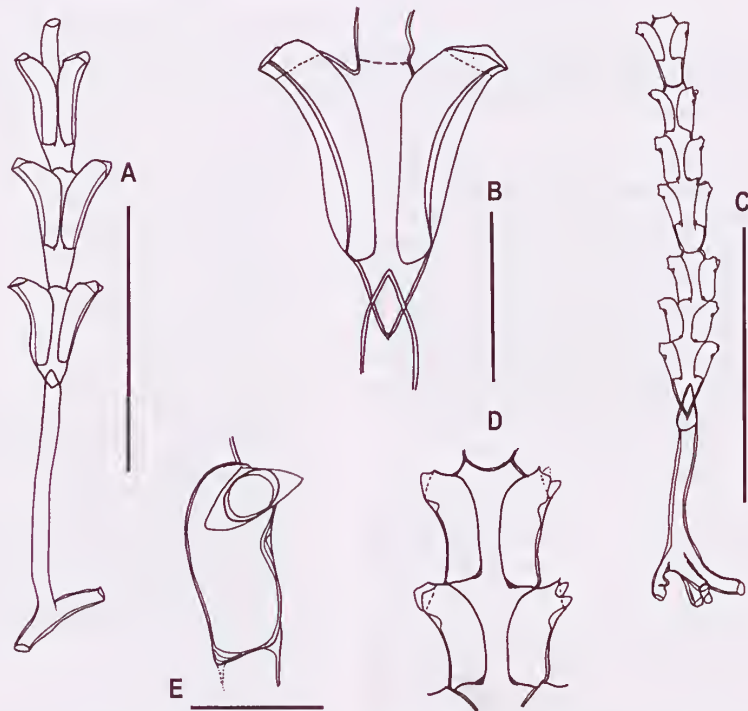


Fig. 10. A, B, *Diphasia digitalis*: A, proximal part of stem. B, proximal stem internode with hinge joint and hydrothecate internode. C - E, *Dynamena quadridentata*: C, stem from colony on aglaopheniid hydroid. D, stem internode. E, hydrotheca showing cusped margin. Scale bars: A, C, 2,000 μ m; B, D, E, 200 μ m.

Description. Stems arising from a creeping tubular hydrorhiza; stems short, unbranched, each bearing three to seven pairs of hydrothecae; proximal stem region athecate, long, tubular, perisarc smooth, ending in a strong hinge joint. Hydrothecae biserial, paired, one pair on internode, node transverse, often indistinct. Hydrothecae long, tubular, expanding from a narrow base at summit of long infrathecal part of internode, adnate adcauline wall twice to three times length of free wall; free wall convex. Abcauline wall concave, sometimes with a slight proximal bulge. Margin quadrangular, perisarc delicate, a low cusp at summit of a longitudinal frontal pleat extending from base of hydrotheca to margin.

Colour. Colourless to pale brown.

Measurements (µm).

Stem		
length athecate	1,280	-1,700
diameter athecate part	160	- 184
length thecate internode	744	- 832
diameter at node	168	- 192
Hydrotheca		
width of pair across base	280	- 296
length adnate adcauline wall	552	- 632
length free adcauline wall	176	- 360
length abcauline wall	640	- 760
width across margin	216	- 240

Remarks. Although the sample is small and the hydrothecal margins are extensively damaged; there is no doubt that the specimen should be referred to *D. digitalis*.

Distribution. Circumglobal in tropical and sub-tropical seas. Australian distribution, Torres Strait (Busk 1852); Queensland (Pennycuik 1959), north-western Australia (Watson 1996).

Genus *Dynamena* Lamouroux, 1812

Dynamena quadridentata (Ellis and Solander, 1786)
(Fig. 10C-E)

Sertularia quadridentata Ellis and Solander, 1786: 57.

Pasya elongata Stechow and Müller, 1923: 469.

Dynamena quadridentata var. *elongata* Billard, 1925: 195. - Yamada 1959: 57. - Pennycuik 1959: 193.

Dynamena quadridentata - Watson 1996: 520.

Record and material. NTM C12911, alcohol preserved material; NTM C12628, MV F86912, microslides, infertile colony on stem of aglaopheniid hydroid, from Stn 87.

Description. Stems simple, straight, to 10 mm high, arising from a tubular, reptant hydrorhiza. Proximal stem region tubular, athecate, perisarc thick, ending in a strong hinge joint; stem thereafter thecate, internodes with three or four pairs of opposite hydrothecae, nodes transverse, collar-shaped, a short infrathecal part below hydrothecal groups. Hydrothecae frontal on stem, laterally separated or sometimes in contact; hydrotheca almost tubiform,

maximum width in distal third, bases and adcauline walls in contact in each internodal group, adnate adcauline wall convex, free part short, concave to convex, abcauline wall concave to margin, a submarginal knob of perisarc below margin; base of hydrotheca flat to slightly concave, a small knot of perisarc at base of adcauline wall. Margin facing outwards, oval, with two almost triangular lateral lobes and a minute adcauline cusp, perisarc thin, an abcauline opercular flap attached to submarginal knob.

Colour. Colourless.

Measurements (µm).

Stem		
length of internode	1,200	-1,500
width at node	136	- 152
diameter of athecate stem	152	- 168
Hydrotheca		
length adnate adcauline wall	324	- 336
length free adcauline wall	56	- 68
length abcauline wall	212	- 256
maximum width hydrotheca	112	- 128
depth of margin (lateral view)	88	- 96
width across marginal lobes (ventral view)	180	- 192

Remarks. Although the hydranth shows no evidence of a caecum, the species is referred to *Dynamena* rather than *Amphisbetia*, a difficulty in interpretation also remarked upon by Billard (1925). The minute adcauline cusp noted by Billard (1925) is visible only in lateral view of the hydrotheca in the present material. *Dynamena quadridentata* is a highly variable species, many varieties having been reported in the past; the present material closely resembles the var. *elongata* previously recorded from Australian waters.

Distribution. *Dynamena quadridentata* is known from the Indonesian region (Billard 1925) the Aru Sea (Stechow and Müller 1923) and Japan (Yamada 1959). In Australia it has been recorded from Western Australia (Stechow 1925, Watson 1996) and Queensland (Pennycuik 1959).

Dynamena bilamellata sp. nov.
(Fig. 11A-E)

Record and material. Holotype, NTM C12957, alcohol preserved material; NTM C12629, NTM C12630, MV F86920, microslides from holotype, infertile colony on red alga, from Stn 87.

Description. Stems simple, monosiphonic, to 10 mm high, arising from a flat, strap-like hydrorhiza; inflexures in perisarc not reaching coenosarc canal. Proximal stem region short, ending in a strong hinge joint, stem internodes thereafter thecate, nodes slender, a transverse collar-like constriction but sometimes with additional hinge joint; infrathecal part widening from node to base of hydrothecae, suprathecal part short.

Hydrothecae biserial, in contact on front of stem, separated behind, facing slightly forward and outward;

base of hydrotheca flat, body tubular, narrowing to margin, adnate adcauline wall parallel to cauline axis, free wall at an angle of 60° to cauline axis, a little shorter than adnate wall, straight to slightly convex, two small spurs pointing downward into infrathecal part at base of adcauline wall; abcauline wall gently concave, slightly tumid near the base with a small submarginal thickening below hydrothecal margin; in older hydrothecae two prominent submarginal shelves project inwards into the hydrotheca from adcauline and abcauline walls. Perisarc of hydrotheca moderately thick.

Margin almost elliptical to subquadrate with two broad lobate cusps midway between adcauline and abcauline walls and a rounded, low adcauline cusp. Operculum pyramidal, low, moderately thick, abcauline valve the larger, adcauline flap divided into two; some margins untidily renovated by regenerated opercular valves. Hydranth stout, with c. 10 tentacles; no abcauline caecum.

Colour. Colourless.

Measurements (µm).

Stem		
distance between hydrothecal pairs	336	- 440
diameter at node	56	- 64
depth of infrathecal chamber	160	- 192
Hydrotheca		
length adnate adcauline wall	92	- 136
length free adcauline wall	80	- 96
length abcauline wall	144	- 160
width across hydrothecal pair at floor	128	- 140
maximum width	84	- 108
width margin (lateral view)	60	- 64

Remarks. The hydrothecal margin is more delicate than the opercular valves so it is often obscured; it is better seen in ventral view. The adcauline marginal cusp is more a change in angle of the rim rather than a true cusp. While the abcauline submarginal shelf is always present in younger hydrothecae, sometimes as a mere thickening of the wall, it is more pronounced in older hydrothecae, where it is produced into a distinct shelf opposite an identical shelf projecting inwards from the adcauline wall. Several stems end in long, trailing, tendrils.

Dynamena bilamellata is related to several species: 1) to *D. cornicina* McCrady (1859) in its strongly opposed cauline nodes, simple, unbranched stems, a tendency towards apical stolonisation and the presence of a submarginal abcauline shelf; there is, however, no mention in the literature of paired abcauline and adcauline shelves in that species, 2) to *D. heterodonta* (Jarvis, 1922) in the presence of opposed shelves and regeneration of the opercular valves but that species is typified by overlapping sets of hydrothecae along the internode and 3) to *D. dalmasi* (Versluys, 1899) (see Calder 1991) in general morphology and in the presence

of opposed submarginal shelves. While fitting some of the above criteria, the hydrocauli of *D. bilamellata* are considerably smaller in all critical dimensions than any of the above species.

Etymology. Named for the two internal submarginal shelves.

Dynamena mertoni (Stechow and Müller, 1923)
(Fig. 12A-G)

Sertularia mertoni Stechow and Müller, 1923: 472.

Records and material. NTM C12910, alcohol preserved material; NTM C12631, MV F86927, microslides, infertile colonies on *Eunice tubifex* from Stn 40. NTM C12909, MV F86934, alcohol preserved material; MV F86926, microslide, colony from Stn 156. NTM C12632, microslide, colony from Stn 52. NTM C12633, microslide, colony from Stn 147. NTM C12634, microslide, colony from wharf piles, Darwin Harbour, coll: J. E. Watson 8/9/1998, depth 6 m, fertile colonies on *Eunice tubifex*. **Other records.** Stn 160. Plater Rock, on compound ascidian and sponge, coll: J. E. Watson, depth 6 m, 22/9/1999.

Description. Hydorrhiza tubular, reptant, and strongly adherent to substrate. Stems to 20 mm high, monosiphonic, pinnate, arising at irregular intervals from hydorrhiza, pinnate, monosiphonic, rather lax, straight or slightly flexuose, lower part of stem athecate, moderately long, perisarc thick, ending in a strong hinge joint. Stem internodes thereafter short, nodes transverse, distinct, internodes becoming narrower distally. First two hydrocladia above hinge joint usually opposite, hydrocladia thereafter alternate, inserted above node at an angle of 70 - 80° to stem axis on short apophyses with transverse distal node varying from a mere constriction to a deep collar; node followed by a short athecate internode with one, sometimes two, deep, distal hinge joints; hydrocladium thecate, inflated beneath hydrothecae, nodes narrow, internodes bearing up to four pairs of hydrothecae.

Hydrothecae biseriate, opposite, seated on front of internode, long, tubular, adnate adcauline walls conjoined, free adcauline wall c. one third length of adnate wall, curved outwards, abcauline wall partly adnate, straight proximally, concave distally, floor of hydrotheca straight to faintly rounded. Hydrothecal margin elliptical (ventral view) with two long, pointed lateral cusps shifted to adcauline side and a minute adcauline cusp, a small submarginal knot of perisarc on abcauline wall, operculum of two valves, adcauline valve with a central rupture line. A cauline hydrotheca in axil of hydrocladium, one above, almost level with distal node and one opposite, halfway along internode. Perisarc of hydrocladia and hydrothecae thin.

Gonothecae grouped on proximal stem, large, barrel shaped, borne on a short, stout pedicel, body faintly corrugated to almost smooth, perisarc moderately thick,

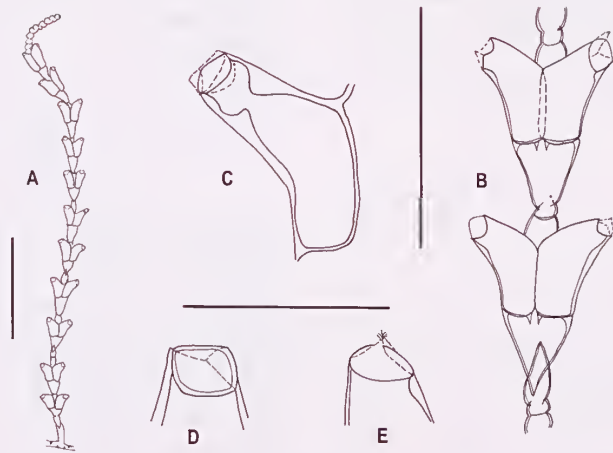


Fig. 11. *Dynamena bilamellata* sp. nov. **A**, stem from holotype colony with apical tendril. **B**, proximal stem internodes with proximal hinge joint. **C**, hydrotheca with submarginal shelves. **D**, **E**, opercular structures. Scale bars: **A**, 1,000 μ m; **B**, 500 μ m; **C**, **D**, **E**, 200 μ m.

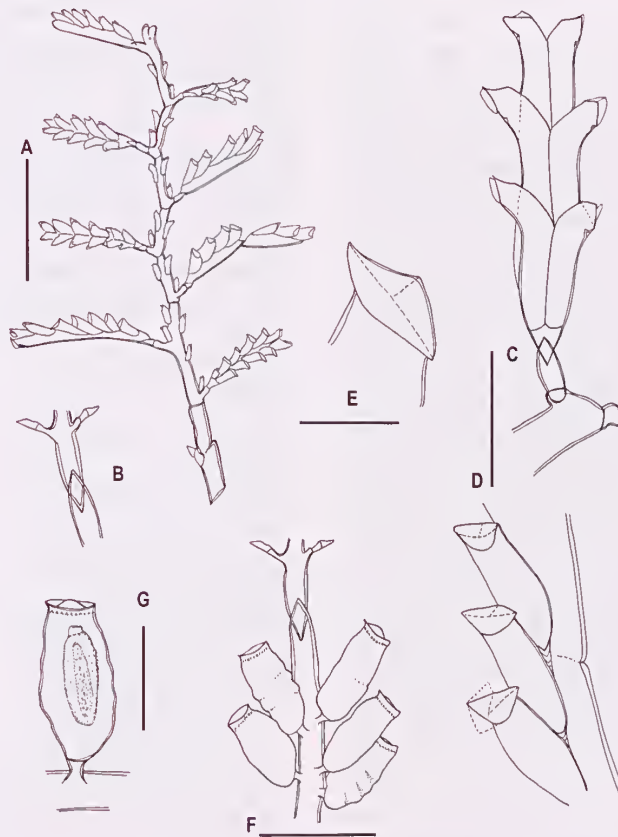


Fig. 12. *Dynamena mertoni*: **A**, infertile stem. **B**, proximal stem with hinge joint and opposite basal hydrocladia. **C**, hydrocladial internode. **D**, ventral view of operculate hydrothecae. **E**, lobate hydrothecal margin with entire operculum. **F**, gonothecae on proximal stem. **G**, gonotheca with planula larva. Scale bars: **A**, **B**, **F**, **G**, 2,000 μ m; **C**, **D**, 500 μ m; **E**, 300 μ m.

orifice distal, circular, inside a short, slightly everted collar, a row of denticles within, operculum a thick, dome-shaped plug. Gonotheca containing a single large planula larva.

Colour. Stems white to almost colourless, gonophores white to pale pink.

Measurements (μm).

Stem	
length of internode	720 - 1,160
diameter of transverse node	200 - 360
Apophysis	
length of adcauline side	40 - 152
width at transverse distal node	88 - 152
Hydrotheca	
length of adnate adcauline wall	400 - 544
length of free adcauline wall	168 - 200
diagonal total length of abcauline wall to embayment	520 - 544
maximum width of hydrotheca	120 - 160
width of margin	
between embayments	120 - 156
width across marginal lobes (ventral view)	220 - 268
Gonotheca	
length, excluding pedicel	1,700 - 1,780
length of pedicel	64 - 80
maximum diameter	800 - 900
diameter of marginal rim	480 - 496

Remarks. Although it is somewhat difficult to extract critical characters and comparative dimensions from Stechow and Müller's (1923) description of *Dynamena mertoni*, I believe the present material is that species.

The abundant present material shows the species should be referred to *Dynamena*. As noted by Stechow and Müller, the perisarc of the lower stem is quite thick with no evidence of polysiphony. In some stems where there are two sets of basal hinge joints there are also two pairs of opposite hydrocladia. Frequently, these hydrocladia are shed, leaving only paired apophyses. In many respects *D. mertoni* resembles *D. cornicina* McCrady, 1858, the differences being: 1) the complete absence of simple stems from the colonies, 2) the grouped overlapping pairs, rather than single pairs of hydrothecae, and 3) opposite hydrocladia above the basal hinge joint. The distal collar of the gonotheca also resembles that figured by Billard (1925) for *D. cornicina*; however, other authors (e.g. Gibbons and Ryland 1989, Millard 1975) have not shown this feature. Unfortunately few authors have given measurements or illustrations of *D. cornicina* thus impeding comparison with doubt arising as to whether all material referred to *D. cornicina* indeed belongs to that species.

There is a strong superficial resemblance between infertile hydrocauli of *D. mertoni* and very young stems of *Idiellana pristis*, especially as colonies of both species often share the same habitat of *Eunice tubifex* (J. E. W., pers. obsv).

This is the second record of *D. mertoni* and first description of the gonotheca. The species is abundant in Darwin Harbour.

Distribution. Previously known only from the Aru Sea (Stechow and Müller 1923).

Genus *Tridentata* Stechow, 1920

***Tridentata* sp.**

(Fig. 13A-C)

Record and material. NTM C12635, microslide, one infertile stem on the polychaete *Eunice tubifex*, Stn 156.

Description. Hydorrhiza a knot of tubes. Stem 5 mm high, monosiphonic, branched, proximal stem region short, athecate, perisarc thick, ending in several transverse constrictions. Proximal thecate region with three pairs of hydrothecae to level of first branch, branching thereafter sub-dichotomous, a hydrotheca in axil of dichotomy; dichotomous internode with a V-shaped to transverse distal node. Hydrothecae paired on internode, subalternate to opposite, frontal on branch internode, pairs separated by a long, slender infrathecal part and a short suprathecal part with deep transverse collar-shaped node. Hydrothecae tubular, narrowing to an upwardly tilted margin; adcauline walls of pair in contact, parallel to branch axis, adnate adcauline wall shorter than free part, free wall convex to almost straight, bent outwards at an angle of 30 - 40° to internode; abcauline wall concave, contiguous with infrathecal chamber, base of hydrotheca variable, flat, slightly convex or concave. Margin with two lateral lobes with deep embayments between and a small adcauline cusp; aperture oval, operculum of two tent-shaped valves, perisarc thin. Hydranth with abcauline caecum and c. 20 tentacles.

Colour. Colourless.

Measurements (μm).

Stem	
width above base	180
Branch	
length of internode	496 - 520
width at node	64 - 80
length of infrathecal part	240 - 256
Hydrotheca	
length of adnate adcauline wall	168 - 200
length of free adcauline wall	
(to embayment)	184 - 224
length of abcauline wall	
(to embayment)	192 - 200
depth of margin (lateral view)	88 - 108
width at margin (ventral view)	120 - 140

Remarks. As the specimen has an abcauline caecum, three marginal teeth, an operculum of two valves and almost opposite hydrocladial hydrothecae it is referred to *Tridentata* (for generic definition and discussion of *Tridentata* see Calder 1991 and Cornelius 1995). In some

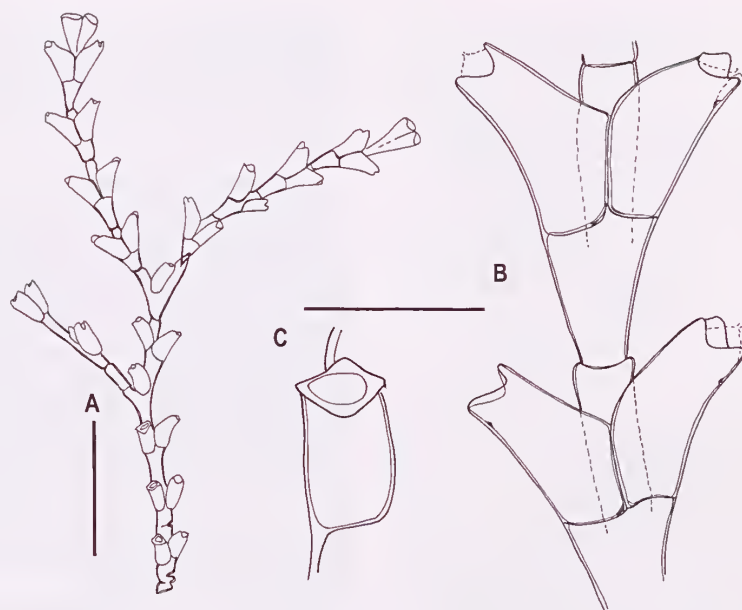


Fig. 13. *Tridentata* sp. A, part of stem. B, stem internodes and hydrothecae. C, hydrotheca, showing lobate margin. Scale bars: A, 1,000 µm; B, C, 300 µm.

malayensis Billard, 1925; however, in that species the lateral cusps are much sharper than those of the present specimen.

Due to the paucity of material and lack of gonosome the species cannot be confidently referred to any known species of *Tridentata*. Neither for the same reasons can it be described as new.

Genus *Idiellana* Cotton and Godfrey, 1942

Idiellana pristis (Lamouroux, 1816)

(Fig. 14A-E)

Idya pristis Lamouroux, 1816: 200. - Allman 1888: 85, 39. - Jäderholm 1916: 16. - Jäderholm 1920: 4. - Jarvis 1922: 344. - Bale 1924: 249.

Idiella pristis - Stechow 1919: 106. - Stechow and Müller 1923: 469. - Briggs and Gardner 1931: 191. - Blackburn 1942: 116. - Vervoort 1946: 306. - Buchanan 1957: 365. - Vervoort 1959: 252.

Idiellana pristis - Cotton and Godfrey 1942: 234. - Pennycuik 1959: 193. - Ralph 1961: 766. - Van Germeden-Hoogeveen 1965: 16. - Vervoort 1968: 36, 103. - Millard 1968: 266. - Hirohito 1969: 21. - Millard and Bouillon 1974: 8. - Millard 1975: 269. - Millard 1978: 194. - Bandel and Wedler 1987: 41. - Vervoort 1993: 188. - Migotto 1996: 65. - Watson 1996: 78.

Dynamena crisioides f. *gigantea* Vannucci, 1946: 558.

Pasythea philippina Marktanner-Turneretscher, 1890: 234, 239.

Records and material. NTM C12874, alcohol preserved material; NTM C12636, MV F86913,

microslides, colony, female colony detached from substrate, Stn 74. NTM C12875, alcohol preserved material, from Stn 7. NTM C12637 microslide, colony on *Eunice tubifex*, from Stn 161. NTM C12876, alcohol preserved material, from Stn 48. MV F86942, alcohol preserved material, from Stn 26. *Other records.* Stns 13, 20, 27, 35, 36, 40, 50, 53, 57, 58, 78, 80, 81, 82, 84, 85, 88, 97, 121, 122, 127, 129, 132, 136, 137, 140, 146, 147, 148, 150, 154, 159, many colonies on *Eunice tubifex* or detached from substrate. Wharf pilings, Darwin Harbour, many colonies on *Eunice tubifex*, coll: J. E. Watson depths 1-10 m, 15-20/8/1998. East Point reefs and Plater Rock, abundant fertile colonies on *Eunice tubifex*, other invertebrates and dead coral. coll: J. E. Watson, depths 1-12 m, 19-22/9/1999.

Description. Hydrorhiza a fibrous mass of thin, tangled stolons. Stems 40 - 170 mm high, monosiphonic, pinnate, sometimes sparingly branched, more or less straight, perisarc of older stems thick, proximal stem region usually athecate with remnant hydrocladia and hydrothecae; stem internodes short, nodes almost transverse, constricted, a hydrotheca in aphophysal axis, a hydrotheca above and one opposite. Hydrocladia alternate, straight, given off at an angle of 70 - 80° from side of stem on lower third of internode; hydrocladial apophysis short with narrow, transverse distal node, hydrocladial internodes bearing up to 10 pairs of hydrothecae, internode beneath hydrothecae inflated.

Hydrothecae biscriate, long, set in an imbricated pattern on front of hydrocladium; adcauline wall convex to sinuous, adnate part overlapping opposite hydrotheca,

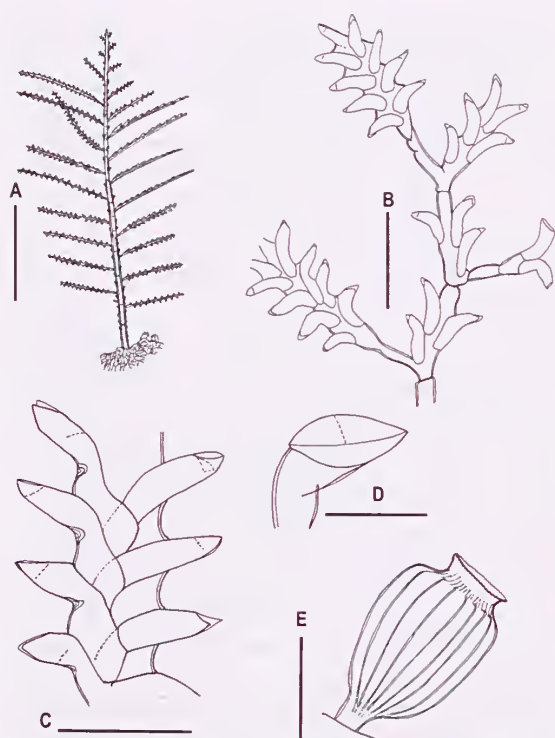


Fig. 14. *Idiellana pristis*: A, stem from young colony. B, part of stem and hydrocladia. C, hydrocladial internode showing imbricated pattern of hydrothecae. D, hydrotheca showing lateral lobes. E, gonotheca. Scale bars: A, 10 mm; B, E, 1,000 µm; C, 500 µm; D, 300 µm.

free part projecting upwards or outwards from hydrocladium. Abcauline wall concave to sinuous, lower third adnate to adcauline wall of hydrotheca below, usually a knot of perisarc at point where wall bends away from hydrocladium. Margin elongate oval with a pair of sharply pointed lateral lobes, embayments between deep, perisarc thin; operculum of two valves, often a pleat in adcauline valve. Hydrothecal perisarc moderately thick. Hydranth buried deep inside sinuous part of hydrotheca.

Gonothecae borne in longitudinal rows on lower to mid-region of hydrocaulus, one on internode; gonothecal pedicel short, wide, body of gonotheca large, urn-shaped, with numerous longitudinal pleats to shoulder, merging into a short, wide, neck, rim everted and sealed by a dome-shaped plug; perisarc of gonotheca very thick. Female gonophore ovoid, containing many large ova.

Colour. Dark honey brown.

Measurements (µm).

Stem	
length of internode	1,300 - 1,700
width at node	500 - 700
distal width of apophysis	160 - 192
Hydrocladium	
length of internode	1,440 - 4,000

width at node	120 - 160
Hydrotheca	
overall length	560 - 768
width across margin (ventral view)	208 - 240
Gonotheca	
overall length	1,700 - 1,740
width across shoulder	940 - 1,120
diameter of margin	580 - 600

Remarks. Due to their imbricating pattern and thickening of the perisarc with age it is difficult to draw or measure individual hydrothecae in older specimens. The Beagle Gulf material includes many young colonies comprising single stems with soft, flexuous perisarc. These differ in so many respects (flexuose stems, axillar hydrothecae on cauline internode and poorly developed imbrication of hydrothecae) that they could well be mistaken for smaller species such as *Dynamena mertonii* (Stechow and Müller, 1923). Intergradations can, however, usually be found among the large range of material. *Idiellana pristis* is one of the most widespread species in the Beagle Gulf.

Distribution. Circumtropical, especially the Indo-Pacific. Recorded from Western Australia (Watson 1996) and tropical Queensland (Pennycuik 1959).

Idiellana lepida sp. nov.

(Fig. 15A-E)

Record and material. Holotype, NTM C12954, alcohol preserved colony, NTM C12638, MV F86915, microslides from holotype, colony on *Eunice tubifex*, Plater Rock, coll: J. E. Watson, depth 3 m, 21/9/1999.

Description. Hydrorhiza tubular, thick, entwining substrate. Stems to 90 mm long, monosiphonic, gracefully plumose, proximal part of stem long, ahydrocladate, nodes if present, transverse, faint; lower stem perisarc thick, thinning distally; two rows of opposite hydrothecae on stem, a distinct internal coenosarc tube running up centre of ahydrocladate stem region.

Hydrocladia alternate, close-set, up to 15 mm long, borne on a short, distinct apophysis directed upwards at an angle of 40° to cauline axis, distal apophysal node a transverse constriction, this followed by an athecate internode with strong hinge joint. Most hydrocladia unsegmented; if segmented, internodes with at least four pairs of hydrothecae, nodes strongly oblique, constricted.

Hydrothecae biseriate, paired, not protruding, tubiform, base of one of pair sometimes slightly displaced downwards with respect to other, each pair slightly overlapping that above, adcauline walls in contact, straight to convex, free length of adcauline wall minute, adcauline wall slightly inturned at base, ending in a small knob of perisarc, abcauline wall almost straight, a small internal submarginal thickening in perisarc. Cauline hydrothecae alternate, same as those on hydrocladia but separated laterally and vertically, one

beside apophysis and two or three in a row above. Margin of hydrotheca facing outward and tilted slightly upwards; margin with two prominent ear-shaped lateral cusps, perisarc thin, aperture oval. Operculum a single very thin adcauline valve. Hydranth without caecum and with 16 - 20 tentacles.

Gonothecae abundant throughout hydrocladial part of stem, borne on caulus or hydrocladia; cauline gonothecha inserted just above hydrocladial apophysis, hydrocladial gonothecae proximal on hydrocladia, arising behind hydrothecal pairs; gonothecha standing erect on a long, bent pedicel with basal constriction or twist, body large, barrel-shaped, faintly undulated to almost smooth, narrowing to a short, wide, slightly out-turned collar, operculum a low domed plug. Perisarc of gonothecha very thick, distal collar of thick, rough strands.

Colour. Pale brown.

Measurements (μm).

Stem

distance between hydrocladia on same side	1,200 - 1,400
width below hydrocladium	320 - 500
width of apophysis at distal node	128 - 144

Hydrocladium

maximum length of internode	5,000
width at node	120 - 160

Hydrotheca

length of adnate adcauline wall	212 - 240
length of free abcauline wall	184 - 224
maximum width	92 - 104
width across margin, between cusps (ventral view)	296 - 312
width of aperture	204 - 212
length of marginal cusp	20 - 24

Gonothecha

overall length	1,060 - 1,200
diameter of collar	400 - 500
length of pedicel	160 - 216

Remarks. Although the hydrothecae appear opposite in front view, from other angles of view they may appear to be subopposite. The adcauline opercular valve is very fragile and although none were found intact, its adcauline position is inferred from fragments of tissue adhering to the adcauline margin, the abcauline margin being invariably free of tissue. Most gonothecae contain a web of strands of tissue throughout the body. The absence of maturing gonophores and intact operculae suggests the gonothecae are immature.

Although it differs in respects such as arrangement and some structures of the hydrothecae, the lack of an abcauline caecum, the paired marginal hydrothecal cusps and an adcauline opercular valve indicates the species should be referred to *Idiellana*, a hitherto monospecific genus.

Only one colony of 24 stems was found, suggesting that *Idiellana lepida* may be a rare species.

Etymology. Refers to the graceful, lax colonies.

Genus *Salacia* Lamouroux, 1816

***Salacia hexodon* (Busk, 1852)**

(Fig. 16A, B)

Pasythea hexodon Busk, 1852: 395. - Bale 1884: 113. - Bale 1888: 771. - Jäderholm 1916: 5.

Salacia hexodon - Billard 1925: 207. - Pennycuik 1959: 194. - Watson 1996: 78.

Records and material. NTM C12928, alcohol preserved material, from Stn 42. NTM C12929, alcohol preserved material; NTM C12640, MV F86910, microslides, colony from Stn 7. NTM C12927, alcohol preserved material, colony from Stn 54. Sparse infertile colonies 20 - 40 mm high, detached from substrate. *Other records.* Stns 20, 89. Plater Rock, small colonies amongst other hydroids on *Eunice tubifex*, coll: J. E. Watson, depth 8 m, 22/9/1999.

Description. Stems monosiphonic, slender, lax, branching irregularly dichotomous, so that no true stem is present; a short internode above each dichotomy and a partially adnate hydrotheca in each axil. Internodes long, tubular, expanding a little distally to proximal

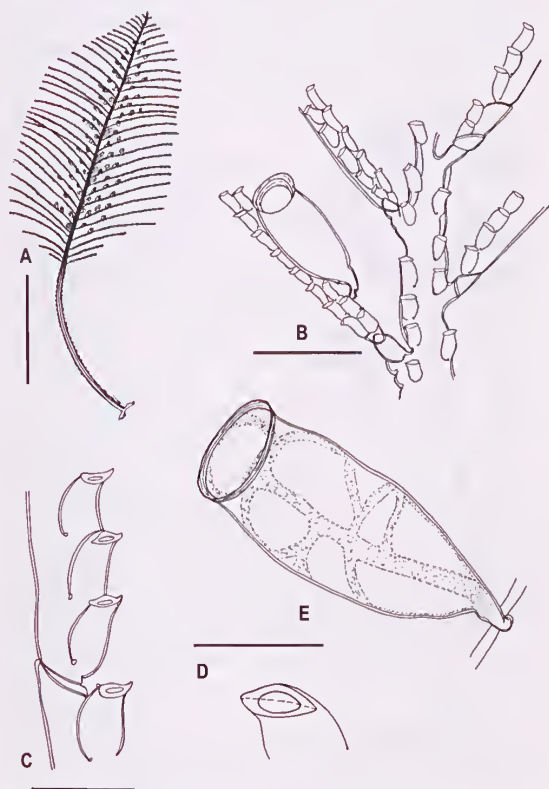


Fig. 15. *Idiellana lepida* sp. nov. A, fertile stem from holotype colony. B, part of stem and hydrocladia. C, hydrocladial internode. D, cusped hydrothecal margin. E, gonothecha. Scale bars: A, 10 mm; B, 1,000 μm ; C, 200 μm ; D, E, 500 μm .

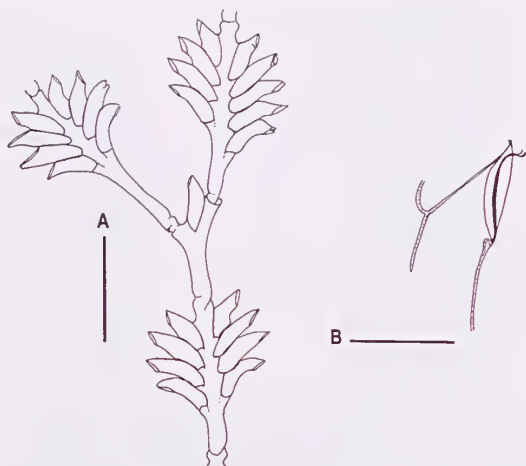


Fig. 16. *Salacia hexodon*: A, part of stem. B, lateral view of operculate hydrotheca. Scale bars: A, 1,000 μ m; B, 300 μ m.

hydrothecae, nodes transverse, collar-like, perisarc moderately thick and smooth throughout.

Hydrothecae biserial, three to five overlapping subopposite pairs, in a crest-like group; hydrothecae separated laterally, more or less tubular, widest about middle, inclined outwards, adnate adcauline wall moderately convex, free part almost same length or shorter than adnate wall; abcauline wall concave, adnate part about same length as free wall; margin slightly sinuate, inclined downwards, closed by a thick abcauline operculum attached to a small internal submarginal peg.

Colour. Colourless to brown.

Measurements (μ m).

Internode	
length	2,150 - 2,300
diameter at node	110 - 180
Hydrotheca	
length of adnate adcauline wall	350 - 500
length of free adcauline wall	280 - 380
length of adnate abcauline wall	300 - 380
length of free abcauline wall	140 - 180
width of margin	240 - 280

Remarks. The distalmost internodes often extend into tendrils although without any evidence of re-attachment to new substrate. This distinctive, straggling species occurs in small colonies of a few stems.

Distribution. A tropical species known from Torres Strait (Busk 1852, Kirkpatrick 1890), Queensland (Bale 1888, Pennycuik 1959), north-western Australia (Jäderholm 1916, Watson 1996) and Indonesia (Billard 1925).

Salacia sinuosa (Bale, 1884)

(Fig. 17A-E)

Thuiaria sinuosa Bale, 1888: 772. - Ritchie 1911: 844. - Levinsen 1913: 271. - Bale: 1914: 12. - Briggs

1914: 294. - Bale 1915: 279. - Mulder and Trebilcock 1914: 9. - Briggs 1918: 38. - Hodgson 1950: 38.

Salacia sinuosa - Stechow 1922: 150. - Stechow 1923: 214. - Billard 1925: 204. - Blackburn 1942: 115. - Rees and Thursfield 1965: 151. - Watson 1994: 66. - Watson 1996: 78.

Records and material. NTM C12926, alcohol preserved material, colony from Stn 156. NTM C12925, MV F86929, alcohol preserved material; NTM C12641, MV F86911, microslides, colonies detached from substrate, Stn 154. *Other records.* Stns 48, 100, 137, 139, 147, 155.

Description. Hydorhiza a tough plug of perisarc up to 20 mm wide. Stems long, the tallest 22 cm high, supple, smooth, strongly fasciated by many fine tubes running more or less parallel up stem to end of branches; lower stem region up to 3 mm thick, unbranched, mid to upper region dichotomously branched in three or more orders of branching in several planes producing a sparse canopy, ultimate branches pinnate, up to 50 mm long and 1 mm diameter at dichotomy, a short proximal length of each branch ahydrocladate, thereafter hydrocladate.

Hydrocladia inserted on prominent, twisted apophyses; three hydrothecae between successive hydrocladia, one axillar and two above, adcauline wall of distalmost adnate to hydrocladium; internodes usually

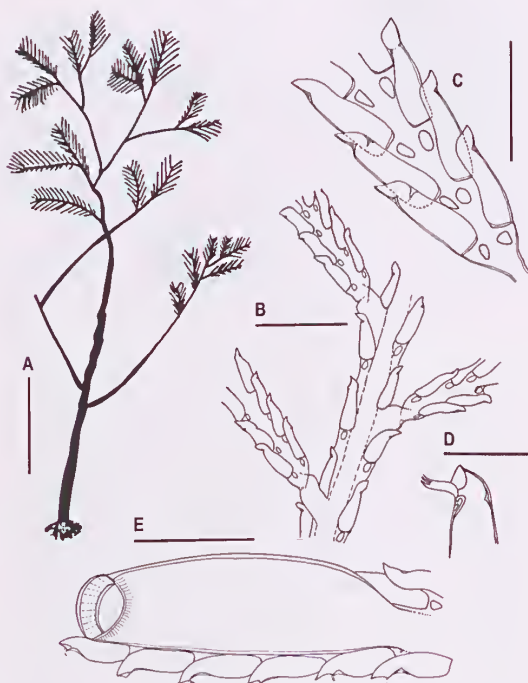


Fig. 17. *Salacia sinuosa*: A, colony of one main stem. B, branch with hydrocladia. C, hydrocladial internode. D, hydrotheca with internal submarginal shelf and operculum. E, gonotheca. Scale bars: A, 100 mm; B 1, 000 μ m; C, E, 500 μ m; D, 200 μ m.

hydrocladia, one axillar and two above, adcauline wall of distalmost adnate to hydrocladium; internodes usually absent but when present, of variable length, nodes strongly constricted.

Hydrothecae biserial, opposite to subopposite, separated transversely, overlapping vertically, tubular, sinuous, narrowing from floor to margin; adcauline wall usually completely adnate, but sometimes a short length free behind margin, a small shelf below margin and a circular to pyriform fenestration below base; abcauline wall almost straight to convex, a shelf in perisarc just below margin. Margin narrow, beak-shaped, inclined obliquely downwards, oblong to subcircular (frontal view), operculum attached to submarginal abcauline shelf. Perisarc of margin and operculum thin, perisarc of branches, hydrocladia and hydrothecae very thick. Hydranth without abcauline caecum.

Gonotheca large, loaf-shaped, inserted without pedicel between rows of hydrothecae, up to six gonothecae along hydrocladium; gonotheca adnate to hydrocladium, sometimes a short part behind margin free, distal end often in contact with base of next, wall smooth (see remarks), orifice distal, circular to subcircular, upturned with a raised thickened rim, a ring of irregularly-shaped denticles inside, operculum a thick plug of tissue.

Colour. Lower stems and branches dark brown to almost black, upper branches and hydrocladia pale brown.

Measurements (µm).

Hydrocladium

distance between hydrocladia	
on same side	1,800 - 2,000
apophysis, length adcauline side	240 - 280
apophysis, width at node	192 - 240

Hydrotheca

depth, adcauline margin to base	432 - 520
width at floor	120 - 176
width at margin (lateral view)	88 - 104

Gonotheca

length	1,340 - 1,520
maximum width	460 - 540
diameter of aperture	256 - 360

Remarks. The colonics conform to descriptions and dimensions given by previous authors. The tough, woody appearance, thick perisarc and dichotomously branched canopy is distinctive. The beak-shaped hydrothecal margin and opercular valve may have up to seven replications.

Billard (1925) could not find in his material the transverse annulations on the gonotheca reported by Bale (1888) and suggested that their absence from his female material may be due to sexual dimorphism. Faint annulations present on the abcauline walls of many Beagle Gulf gonothecae can only be seen in preserved

material but become invisible in cleared and mounted specimens.

This species is abundant in deeper water in Beagle Gulf. It was not found in the shallower waters of Darwin Harbour.

Distribution. Indonesia (Billard, 1925). Better known from Australian waters: Queensland (Bale 1888), central coast of New South Wales (Ritchie 1911), Great Australian Bight and Tasmania (Briggs 1914, Hodgson 1950), Western Australia (Watson 1996).

Salacia tetracythara Lamouroux, 1816

(Fig. 18A-F)

Salacia tetracythara Lamouroux, 1816: 212. - Lamouroux 1821: 15. - Stechow 1913: 30. - Stechow 1922: 150. - Thornely 1916: 146. - Thornley 1924: 54. - Billard 1925: 202. - Mammen 1965: 54. - Pennycuik 1959: 194. - Rees and Vervoort 1987: 103. - Gibbons and Ryland 1989: 414. - Hirohito 1995: 183.

Thuiaria fenestrata Bale, 1884: 116. - Bale 1888: 773. - Kirkpatrick 1890: 604. - Nutting 1905: 950.

Calypthothuiaria opposita Von Campenhausen, 1896: 312.

Thuiaria tetracythara - Billard 1909: 319.

Records and material. NTM C12930, MV F86943, alcohol preserved material; NTM C12642, microslide, colony from Stn 126. NTM C12932, alcohol preserved material, colony from Stn 155. NTM C12931, alcohol preserved material; NTM C12643, MV F86909, microslides, colony from Stn 81. All fertile colonics, on dead bryozoans, sponge and shale. *Other record*, Stn 152.

Description. Tangled colonies to 100 mm high and 100 mm wide ranging from groups of simple, stiffly pinnate stems to a large fan-shaped colony of many intergrown stems with one or two orders of branches arising from a thick, ramified hydrorhiza. Stems up to 2 mm thick at base, stems and major branches fascicled, perisarc thick. Branch internodes visible only on younger, monosiphonic regions, nodes a transverse constriction, each internode with a hydrocladium and three hydrothecae, one axillar, one opposite and one below hydrocladium.

Hydrocladia long, monosiphonic, held out stiffly at an angle of c. 60° to axis of branch from a broad apophysis; apophysis with an indistinct, constricted, distal node; hydrocladial internodes usually absent but when present, with 2-6 pairs of hydrothecae.

Hydrothecae biserial, immersed in hydrocladium, subopposite, laterally separated, overlapping vertically, long, tubular, narrowing from floor to margin; adcauline wall convex, convexity increasing distally, adcauline wall almost entirely adnate to internode, a very short free part just behind margin, abcauline wall straight to concave, floor of hydrotheca incurved to accommodate a thin circular to ovoid adcauline fenestration. Hydrothecal

one median adcauline cusp, in anterior view margin sub-circular; operculum a single abcauline flap attached to a small internal submarginal peg, perisarc of operculum delicate.

Gonotheca large, globular, up to six in an upright row along hydrocladium, pedicel short, perisarc very thick, smooth, aperture surmounted by a raised collar with vertical striations and a basal ring of large, internal, inwardly pointing denticles; operculum a thick plug of tissue.

Colour. Pale brown.

Measurements (μm).

Branch		
length of internode	800	- 980
width at node	168	- 208
Hydrocladial apophysis		
length, adcauline side	80	- 88
width at node	88	- 144
Hydrotheca		
depth abcauline margin to base	384	- 440
maximum width	128	- 136
width at margin (lateral view)	120	- 128
Gonotheca		
overall length	1,040	- 1,060
maximum width	760	- 860
diameter of aperture	520	- 540

Remarks. The material conforms to descriptions of *Salacia tetracythara* by previous authors. In monosiphonic parts of the branches the hydrocladial internodes are faintly flexuose, but this character is lost in older, polysiphonic parts of the stems. In younger branches the hydrocladial apophyses are sometimes quite long, extending 250 μm from the hydrocaulus to the base of the first hydrothecal pair. In large colonies the branches and hydrocladia are heavily intergrown and in some instances hydrocladia have extended and reversed direction of growth, becoming attached to the substrate. The marginal cusps of the hydrotheca are frequently damaged or obscured by opercular tissue and are thus difficult to see. While many gonothecae are empty, maturing gonophores suggest the colonies are probably male.

The hydrothecae of *Salacia tetracythara* superficially resemble those of *S. sinuosa*, however, the species are easily distinguished by colony form and shape of the gonotheca.

Distribution. Indian Ocean (Rees and Vervoort 1987), Indo-Pacific (Billard 1925; Ryland and Gibbons 1989), Japan (Hirohito 1995). Torres Strait (Kirkpatrick 1890), Australian tropical to temperate east and south-east coast (Bale 1884, 1888; Pennycuik 1959).

Salacia flavidula sp. nov.
(Fig. 19A-D)

Records and material. Holotype, NTM C12959, alcohol preserved material; NTM C12644, microslide

from holotype colony. Paratypes, NTM C12645, alcohol preserved material, MV F86925, microslide. Colonies on *Eunice tubifex*, Plater Rock, coll: J. E. Watson, depth 3 m, 22/9/1999.

Description. Stems up to 20 mm long, plumose, lower ahydrocladial stem region short, perisarc thick, lightly fascicled by two or three stolonal tubes which may reach proximal node; proximal node a blunt hinge joint, hydrocaulus thereafter monosiphonic, segmented, hydrocladial. Cauline internodes short, nodes transverse, deeply indented, a pair of opposite hydrocladia inserted on a wide shoulder-like apophysis above proximal node; two pairs of opposite or subopposite hydrothecae above hydrocladia, bases of hydrothecae not in contact across stem. Hydrocladial apophysis with a deep transverse proximal node and usually a secondary transverse node, sometimes a shallow V-shaped distal node. Hydrocladium broad, inflated below hydrothecae, perisarc very thin, ending in a blunt distal tip; hydrocladium usually entirely lacking nodes, but if present, represented only by a faint constriction in perisarc.

Hydrothecae biserial, alternate, sessile, frontal on hydrocladium, tubiform, narrowing to margin, adcauline wall convex, adnate to hydrotheca above, abcauline wall concave to almost straight, base of hydrotheca flat, concave or convex, partially overlapped by hydrotheca above. Adcauline margin of hydrotheca almost straight, a pair of lateral lobate cusps flanking margin, abcauline marginal embayment with a thin opercular valve.

Hydrocladial coenosarc and hypostome of hydranth containing numerous large bean-shaped haplonemes, none discharged. Hydranth with c. 24 tentacles, no abcauline caecum.

Colour. Brilliant lemon yellow in life; brown when preserved.

Measurements (μm).

Stem		
length of internode	960	- 100
width at node	224	- 352
Apophysis		
length (adcauline side) to distal node	136	- 240
width at proximal node	184	- 200
Hydrocladium		
maximum length		8,000
depth behind hydrothecae	168	- 296
length of internode	2,400	- 3,700
width at node	160	- 176
Hydrotheca		
length (diagonal) adcauline wall		
margin to base	360	- 400
length free abcauline wall		
(lateral view)	240	- 264
width margin across cusps	128	- 160
Nematocysts		
length	22	- 28
width	8	- 10

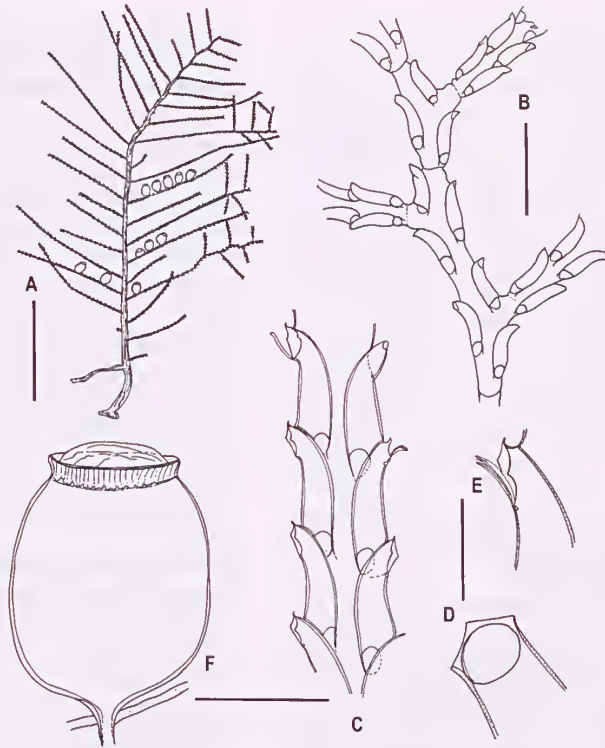


Fig. 18. *Salacia tetracythara*: A, fertile colony. B, hydrocladate part of stem. C, hydrocladial internode. D, ventral view of hydrotheca showing marginal cusps. E, operculate hydrotheca. F, gonotheca with operculum. Scale bars: A, 10 mm; B, 1,000 μ m; C, F, 500 μ m; D, E, 200 μ m.

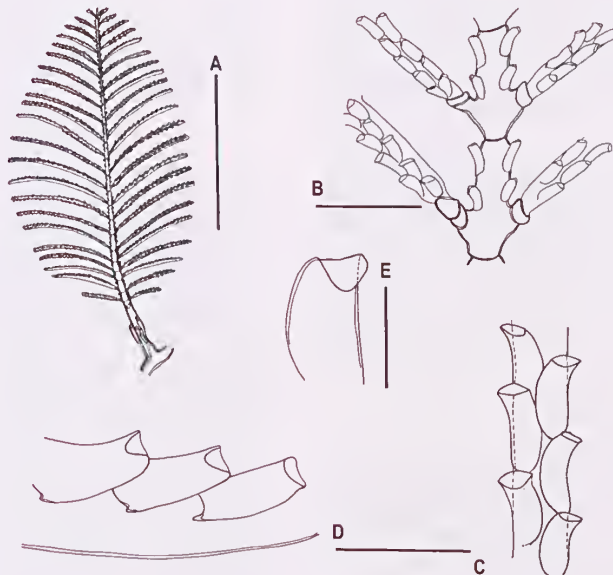


Fig. 19. *Salacia flavidula* sp. nov. A, stem from holotype colony from Plater Rock. B, part of stem with opposite hydrocladia. C, part of hydrocladium. D, lateral view of hydrocladium showing overlapping hydrothecae. E, frontal view of hydrotheca showing lobate cusps. Scale bars: A, 10 mm; B, 1,000 μ m; C, D, 500 μ m; E, 200 μ m.

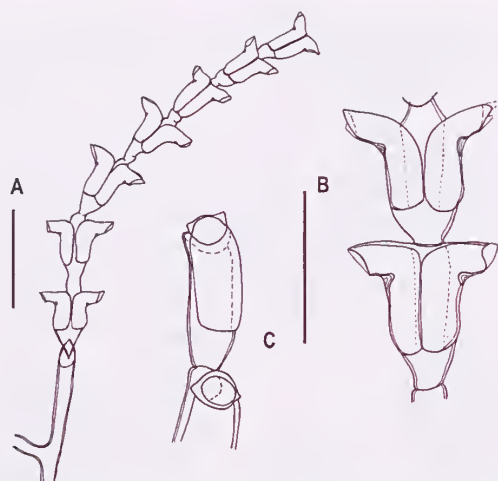


Fig. 20. *Salacia alata* sp. nov. A, stem from holotype colony. B, stem internodes. C, view of hydrothecae showing marginal cusps. Scale bars: A, 1,000 µm; B, C, 500 µm.

Remarks. Although the colonies are quite stiff in life, the hydrocaulus becomes lax and fragile when preserved. While some species of hydroids have opposite proximal hydroeladia, few have opposite hydroeladia throughout the entire hydrocaulus. The intense yellow colour is imparted by an abundant flora of zooxanthallae in the coenosare; this flora was so resistant that it was difficult not to destroy important diagnostic features of the perisarc by pre-mounting clearing agents. As the material was initially preserved in formaldehyde solution the nematocysts could not be discharged, and so could not be further identified. While the hydrothecae have quite distinct marginal cusps, a feature unusual in *Salacia*, the absence of a caecum and presence of an abeauline opereulum indicate the species should be referred to that genus.

Salacia flavidula forms spectacular yellow colonies of up to 30 stems on tubes of the polychaete *Eunice tubifex* growing on coralline boulders in shallow water, the stems of the hydroid arching out gracefully from the substrate. *Salacia flavidula* was found only at Plater Rock.

Etymology. Refers to the distinctive pale yellow colonies.

Salacia alata sp. nov.

(Fig. 20A-C)

Record and material. Holotype, NTM C12646, NTM C12647, MV F86914, microslides from holotype; infertile colony on red alga on *Eunice tubifex*, Stn 40. (All material mounted on microslides; no preserved holotype material remaining).

Description. Hydorrhiza tubular, reptant on alga. Stems simple, to 12 mm high, monosiphonic, proximal stem tubular, of same diameter as hydorrhiza, athecate,

of variable length, ending in a strong hinge joint; perisarc moderately thick, smooth. Stem internodes short, nodes transverse, collar-shaped, sometimes indistinct, a pair of hydrothecae on each internode, infrathecal and suprathecal parts short. Hydrothecae biserial, opposite, tubiform, narrowing distally, adcauline walls in contact in front, separated behind, conjoined part straight to convexly curved, of variable length, free adeauline wall bending sharply outwards to become almost perpendicular or at obtuse angle to cauline axis, abeauline wall straight, a thick shelf of perisarc in flexure. Margin of hydrotheca tilted downwards at c. 45° to cauline axis with two small opposite lateral cusps, aperture sub-circular, sometimes a remnant of abeauline opercular flap inside, marginal perisarc thin. Hydranth without caecum, with 16 - 20 tentacles

Colour. Pale honey brown.

Measurements (µm).

Stem

length of athecate section	560 - 2,000
length of thecate section	2,600 - 9,000
diameter of athecate section	120 - 128
length of thecate internode	560 - 600
width at node	88 - 112

Hydrotheca

length of fused adeauline wall	304 - 376
length of free adeauline wall	200 - 272
width at margin (lateral view)	112 - 140
diameter of margin (frontal view)	120 - 160

Remarks. *Salacia alata* resembles *Salacia dubia* Billard, 1922, but in that species the hydrothecae are conical, not tubular, not bent acutely outwards and the species lacks an internal abeauline shelf.

Etymology. Refers to the sharply bent wing-shaped hydrothecae.

Salacia bidentata sp. nov.

(Fig. 21A, B)

Record and material. Holotype, NTM C12648, microslide, a small colony of three stems on *Eunice tubifex*, Stn 132 (All material mounted).

Description. Hydorrhiza reptant on substrate, stems monosiphonic, straight, proximal athecate region long, tubiform, perisarc smooth, moderately thick, ending in a strong hinge joint. Stem hydrothecate above joint, hydrothecae biserial, opposite, proximal internodes with a pair of hydrothecae, succeeding internodes bearing two to four pairs of hydrothecae, nodes transverse to V-shaped, infrathecal segment immediately above node variable in length, others segments short. Hydrothecal pairs laterally separated in proximal stem region, adjoining walls becoming fused in distal part of stem. Hydrothecae tubular, narrowing behind margin, floor curved to straight, a small knot of perisarc at base of adcauline wall; adnate adcauline wall straight to slightly convex, free wall about one quarter length of adnate part,

curved upwards to margin, a small submarginal plug of perisarc projecting into hydrotheca; proximal abcauline wall straight to slightly concave, curvature increasing at flexure, a large hook-shaped or triangular submarginal shelf in bend projecting into hydrotheca. Margin with two blunt, wing-shaped lateral cusps, perisarc very thin, remnants of a thin abcauline opercular flap inside many hydrothecae. Hydranths well preserved, without caecum, deeply withdrawn into hydrotheca, body closely transversely wrinkled, approximately eight tentacles with distinct rings of nematocysts.

Colour. Pale transparent yellow (preserved material).

Measurements (μm).

Stem

length of athecate stem	1,500
diameter of athecate stem	96 - 112
diameter at node	56 - 112

Hydrotheca

width across pairs at base	144 - 240
length of adnate adcauline wall	256 - 320
length of free adcauline wall	64 - 88
width of margin	72 - 80
length of abcauline shelf	40 - 56

Remarks. Although the colony consists of only a few stems the large abcauline submarginal shelf and adcauline peg distinguishes *Salacia bidentata* from other species of *Salacia*. One stem shows evidence of breakage and regrowth below the hinge joint and another bears a hinge joint in the mid-stem region (Fig. 21A).

Etymology. Refers to the two internal submarginal cusps.

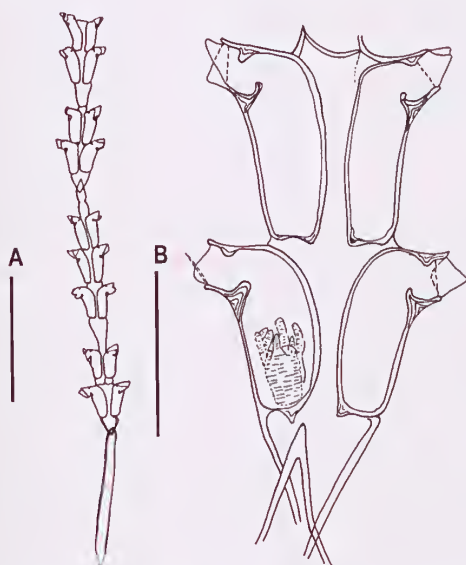


Fig. 21. *Salacia bidentata* sp. nov. A, stem from holotype colony. B, internode showing cusped hydrothecal margin, opercular structures and triangular submarginal shelf. Scale bars: A, 1,000 μm ; B, 500 μm .

Genus *Sertularella* Gray, 1848

There are three closely related species of *Sertularella* in the Beagle Gulf collection. These are: *S. decipiens* Billard 1919, *Sertularella diaphana* (Allman, 1885) and *S. quadridens* (Bale, 1884). These species are also closely related to *S. pinnata* (Lamouroux, 1816), a southern Australian species not found in the Beagle Gulf. The type locality of *S. diaphana* and *S. quadridens* is Moreton Bay on the subtropical Australian east coast, both species now being widely reported from the Indo-Pacific and *S. decipiens* has been previously reported from Indonesia and the Arafura Sea. In order to form a basis for distinction between the species of this group, material from the Beagle Gulf and other Australian localities, specimens in the collection of the Museum of Victoria, Australia, and in the author's private collection, were examined.

***Sertularella decipiens* Billard, 1919**

(Fig 22 A-E)

Sertularella decipiens Billard, 1919: 21. - Billard 1925: 155.

Records and material. NTM C12916, MV F86932, alcohol preserved material; NTM C12964, microslide, colony from Stn 154. NTM C12918, alcohol preserved material; NTM C12965, microslide, colony from Stn 40. NTM C12917, alcohol preserved material; NTM C12963, MV F86919, microslides, colony from Stn 147. Fertile and infertile colonies on *Eunice tubifex*. Other record, Stn 153.

Description. Hydorhiza reptant on substrate, tubular, smaller in diameter than hydrocaulus. Stems to 30 mm high, stiffly pinnate, monosiphonic, perisarc thick, sometimes secondary branching; stem thecate almost from base, divided into short internodes, nodes oblique, deep, tilted parallel with hydrocladium below; three hydrothecae on internode, one axillar, one below hydrocladium and one opposite. Hydrocladia to 12 mm long, given off alternately at an angle of c. 60° halfway up cauline internode from a short apophysis, usually marked by a distinct constriction in perisarc, constriction deeper on proximal side of hydrocladium. Hydrocladial internodes may or may not be present, but if present, bearing three to six hydrothecae on each side, node an oblique constriction in perisarc.

Hydrothecae subopposite to almost opposite, immersed in internode, cauline hydrothecae well separated, close, but not in contact on hydrocladium, margin of one reaching about halfway along adcauline wall of that opposite; hydrotheca more or less tubular, narrowing a little to margin, adcauline wall shallowly convex, usually completely adnate but sometimes a very short free part; abcauline wall almost straight and parallel to hydrocladial axis, bending outwards just below margin, a small shelf of perisarc projecting into hydrotheca at point of

cladial axis, bending outwards just below margin, a small shelf of perisarc projecting into hydrotheca at point of flexure; ratio of length of abcauline to adcauline wall 1: 1.4 - 1.8, base of hydrotheca flat to slightly convex, a knot of perisarc projecting downwards into internode from base of wall. Margin tilted upwards at an angle of 25° - 30° to hydrocladial axis with four low, equidistant, sharp cusps, one adcauline, one abcauline and two lateral, separated by wide, shallow embayments; operculum of four valves. Margin not replicated.

Gonothecae borne on hydrorhiza and lower stem, long, sausage-shaped, straight or curved, perisarc very thick, pedicel variable in length, crumpled to almost straight, body of gonotheca encircled by 8 - 10 deep corrugations usually deepest about middle, fading out proximally but some gonothecae merely undulated throughout; aperture a shallow, transverse depression surrounded by four low cusps, operculum of four valves. Female gonophore ovoid, containing many large ova.

Colour. Live colonies pale yellow.

Measurements (µm).

Hydrorhiza, diameter	160
Stem	
diameter at node	340 - 640
Hydrocladium	
length of apophysis, abcauline side	104 - 240
diameter at proximal node	200 - 280
Hydrotheca	
length of adcauline wall	600 - 624
length of abcauline wall	336 - 448
maximum width	256 - 336
diameter at margin	200 - 216
Gonotheca	
length excluding pedicel	2,580 - 2,800
length of pedicel	100 - 600
maximum diameter	740 - 980
diameter of aperture	640 - 780

Remarks. In fertile colonies, ova are not only present in the gonothecae but are also distributed throughout the coenosarc; whether this is a normal character of the species or occurred during preservation could not be determined.

In absence of the gonosome, *S. decipiens* can be distinguished from other members of the species group by the longer hydrotheca with distal outward bend, the small submarginal shelf at the point of flexure and the low inclination of the margin to the hydrocladial axis.

Stechow and Müller (1923) doubted the validity of *S. decipiens* suggesting it may be conspecific with *S. quadridens*. While the gonotheca of *S. decipiens* closely resembles that of *S. quadridens* it is almost twice as long as that of *S. quadridens* figured by Weltner (1900) and Billard (1925), and described by Stechow and Müller (1923). For this reason *S. decipiens* is considered a valid species, albeit closely related to *S. quadridens*. Stems of

S. decipiens are shorter, less tidily arranged and are a paler yellow than those of *S. quadridens* and *S. diaphana*. Colonies of *S. decipiens* usually comprise a few stems in a preferred habitat near the base of the tubes of the polychaete *Eunice tubifex*.

Distribution. Indonesia (Billard 1919, 1925). Not previously recorded from Australia.

Sertularella quadridens (Bale, 1884)

(Fig. 23A-F, Table 3)

Thuiaria quadridens Bale, 1884: 119. - Bale 1888: 772. - Bale 1924: 242. - von Lendenfeld 1885b: 915. - Hartlaub 1900: 120. - Weltner 1900: 586. - Ritchie 1910: 818. - Billard 1910: 11. - Billard 1925: 150. - Jäderholm 1916: 6. - Stechow and Müller 1923: 471. - Vervoort 1941: 214. - Vervoort 1946: 314. - Ralph 1961: 830. - Rees and Thursfield 1965: 135. - Mammen 1965: 38. - Pennycuik 1959: 195.

Thuiaria vineta Allman, 1888: 68.

Records and material. NTM C12919, MV F86941, alcohol preserved material; NTM C12967, MV F86918, microslides, colony from Stn 97. NTM C12968, microslide, colony from Stn 138. NTM C12966, microslide, colony from Stn 136. NTM C12920, alcohol preserved material, East Point reef, Darwin, depth 7 m, coll: J. E. Watson, 19/9/1999. East Point reef, Darwin, depth 7 m, coll: J. E. Watson 17/8/1998, large infertile colony. NTM C13079, microslide, Plater Rock, coll: J. E. Watson, depth 8-10 m, 21/9/1999, large fertile colonies on *Eunice tubifex*. *Other record.* Stn 159.

Description. Hydrorhiza a bunch of tubular stolons; stolons creeping up stems to proximal hydrothecae but not forming fasciculations. Stems monosiphonic, pinnately branched in one plane, to 110 mm high, lower stem perisarc thick, thinning distally, hydrocladia up to 10 mm long, given off alternately from proximal part of stem internode, nodes deep, transverse to oblique, inclined opposite directions; three hydrothecae on internode between each hydrocladium, one in axil below node, one opposite and one below hydrocladium, axillar hydrotheca narrow at base, adcauline wall becoming free at or just below junction with cauline node.

Hydrocladia arising from apophysis in top third of internode, proximal part with several constrictions in perisarc, internodes variable in length bearing two to five hydrothecae on each side, nodes deep, transverse to slightly oblique. First hydrocladial hydrotheca on lower side of hydrocladium, hydrothecae thereafter sub-alternate, not in contact, tubiform to flask-shaped, widest about middle, adcauline wall gently convex or sometimes with a slight flexure where adcauline wall becomes free, wall two thirds to almost entirely adnate; free wall (when present) continuing curve of adnate part. Abcauline wall almost straight or a shallow sinuous curve, a short outward deflection of the wall just below margin; length:

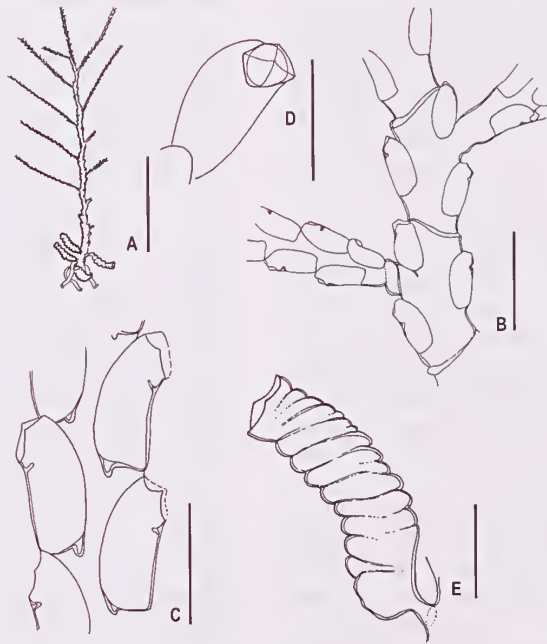


Fig. 22. *Sertularella decipiens*: A, stem from fertile colony. B, hydrocladia. C, hydrothecae on hydrocladium. D, quadrate hydrothecal margin and operculum. E, gonotheca. Scale bars: A, 10 mm, B, E, 1,000 µm; C, D, 500 µm.

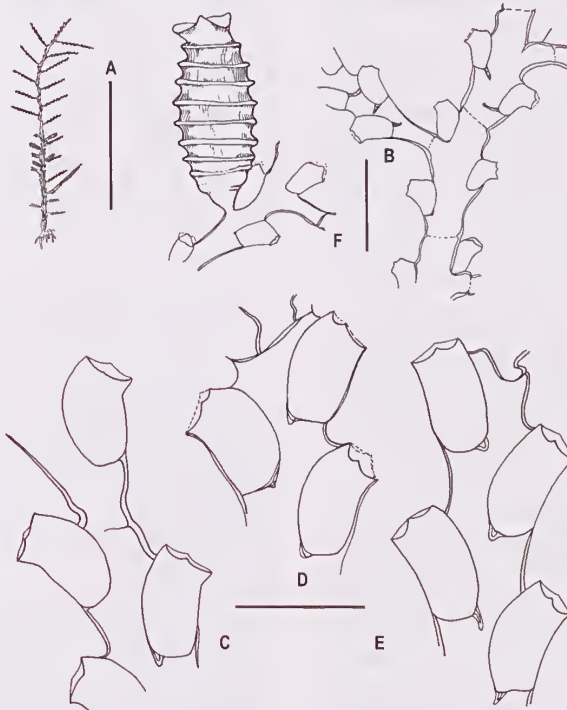


Fig. 23. *Sertularella quadridens*: A, fertile colony from Plater Rock. B, hydrocladial part of stem from same colony. C, hydrocladial internode from same colony. D, E, two hydrocladial internodes with differing hydrothecae from microslide from Peel Island, Queensland (microslide from Bale collection, Museum of Victoria). F, gononotheca from colony from Plater Rock. Scale bars: A, 300 mm, B, F, 1,000 µm; C - E, 500 µm.

wall free than hydrocladate hydrothecae. Floor of hydrotheca flat, thick, in mature hydrothecae a knot of perisarc at base of adcauline wall often extending into a spur. Margin circular, tilted upwards at an angle of 30° - 45° to hydrocladial axis with four equidistant low, pointed cusps, one adcauline, one abcauline and two lateral, rim thickened, operculum of four equal triangular, fairly thick flaps; margin not replicated.

Gonothecae large, borne below hydrothecae in mid-stem region; gonotheca slender, barrel-shaped, pedicel contiguous with body, perisarc thick, with eight deep, widely separated annular flanges passing around body, these fading out proximally; body between flanges finely vertically striated, distal end wide, tubular, orifice large, depressed into apex with four prominent equidistant, outwardly turned protuberances, operculum not visible, gonophore female.

Colour. Live colonies golden yellow.

Remarks. I have compared microslides of *Sertularella quadridens* Bale 1884 from Peel Island, Moreton Bay, Queensland, held in the collection of the Museum of Victoria, Melbourne with the Beagle Gulf specimens (see Table 3). The Beagle Gulf specimens are microscopically identical with a microslide preparation labelled "*Thuiaria quadridens* Bale, Near Peel Island, Moreton Bay, 1886" held in the Bale collection of the Museum of Victoria. *Sertularella quadridens* is

redescribed from both the type and Beagle Gulf specimens.

The Beagle Gulf specimens are taller than the 25 - 50 mm length of stems reported by Bale (1884) but are within the size range given by Billard (1925) for material from Indonesia. The Beagle Gulf specimens have stout stems and thick perisarc, in younger stems the cauline nodes are a shallow constriction and may be altogether absent from older, thicker stems. The basal adcauline spurs described by Bale (1884) and mentioned by Billard (1925) are very well developed below some cauline hydrothecae in the Beagle Gulf specimens. These finger-like spurs are extensions of the adcauline wall, are sometimes forked and occasionally pass completely across the hydrocaulus to connect with the hydrotheca opposite. Both the type and present specimens have a variable length of adcauline wall free of the internode, ranging from none to one third of the total adcauline length. The distance between successive hydrothecae along the hydrocladium and laterally across the hydrocladium is highly variable in the Beagle Gulf material, in some colonies successive hydrothecae are well separated while in others the margin of one overlaps the base of that above. As in the type, some cauline hydrothecae are outwardly bent, widest in the distal half to one third and become decidedly narrow towards the margin; the marginal rim is noticeably thicker in the present specimens than in the type. The ratio of length of abcauline to adcauline wall of 1:1.7 is greater in the present material than in the type.

Bale's type material is infertile, the gonotheca being first described by von Lendenfeld (1885b) from Timaru, New Zealand and later from Indonesia (Weltner 1900, Billard 1925), the Arafura Sea (Stechow and Müller 1923) and Cape Jaubert, Western Australia (Jäderholm 1916).

Billard (1925) erected the variety *Sertularella quadridens* var. *cornuta* (for *S. polyzonias* var. *cornuta* Ritchie, 1910) which was also recognised by later authors (e.g. Vervoort 1993), to accommodate the considerable longitudinal separation of hydrothecae and greater length of internode than present in typical *S. quadridens*. The greatly elongated internode together with a much longer free adcauline hydrothecal wall, replication of the margin and absence of a knot of perisarc at the base of the adcauline wall suggest that the var. *cornuta* may actually be a distinct species.

Fertile colonies from Darwin Harbour occurred mainly on the tubes of the polychaete *Eunice tubifex* on which substrate their golden colour is quite distinctive.

Distribution. *Sertularella quadridens* is widely distributed throughout the Indo-Pacific and Indonesia. Australian distribution: Queensland (Bale 1884, Pennycook 1959), Cape Jaubert, Western Australia (Jäderholm 1916).

Table 3. Measurements (µm) for *Sertularella quadridens*: comparison of Beagle Gulf specimens with type from Queensland.

	Type from Peel Island	Beagle Gulf and Darwin
Stem		
Length of internode	1,560 - 1,800	1,200 - 1,660
width at node	340 - 440	224 - 640
length adnate adcauline wall stem hydrotheca	344 - 440	360 - 408
length free adcauline wall stem hydrotheca	144 - 216	160 - 200
Hydrocladium		
length of internode	1,740 - 2,000	980 - 1,860
width at node	200 - 320	200 - 340
width at apophysis	136 - 200	140 - 320
distance to first hydrotheca (proximal side)	600 - 760	280 - 700
Hydrotheca (hydrocladium)		
length of adnate adcauline wall	400 - 480	300 - 464
length of free adcauline wall	40 - 144	120 - 200
length of abcauline wall	376 - 384	320 - 384
width at base	168 - 200	144 - 184
maximum width	232 - 288	256 - 280
diameter at margin	240 - 280	192 - 224
Gonotheca		
length including pedicel	-	1,960 - 2,200
maximum width	-	760 - 820
length of pedicel	-	220 - 240
width of pedicel, proximal	-	140 - 180
depth of ridge	-	120 - 152

Sertularella diaphana (Allman, 1885)

(Fig. 24A-E)

Thuiaria distans Allman, 1877: 27 [secondary homonym; not *Dynamena distans* Lamouroux, 1816].

Thuiaria pinnata Allman, 1877: 28 [secondary homonym; not *Sertularella pinnata* Clark, 1876].

Thuiaria diaphana Allman, 1885: 145.

?*Thuiaria hyalina* Allman, 1888: 69.

Sertularella distans Hartlaub, 1901: 100. - Nutting 1904: 88. - Vervoort 1968: 104.

Sertularella pinnigera Nutting, 1904: 86. - Hartlaub 1901: 113. - Deevey 1954: 270. - Vervoort 1968: 105.

Sertularella torreyi Nutting, 1905: 934, 949.

Sertularella speciosa Congdon, 1907: 463. - Bennett 1922: 250. - Fraser 1943: 92. - Deevey, 1954: 270. Vervoort 1968: 44, 105. - Wedler 1975: 333. - Cooke 1977: 96. - Colin 1978: 139. - Bandel and Wedler 1987: 38. - Flórez-González 1983: 120.

Sertularella tridentata Stechow, 1913: 137. - Stechow 1925: 226.

Sertularella diaphana - Bale, 1919: 337. - Jäderholm 1920: 6. - Billard 1925: 157. - Stechow 1925: 226. - Billard 1931: 248. - Billard 1933: 12. - Dollfus 1933: 127. - Millard 1958: 188. - Yamada 1958: 58. - Yamada 1959: 63. - Pennycuik 1959: 195. - Hirohito 1969: 21. - Millard 1970: 268. - Schmidt 1972:

42. - Millard 1975: 285. - Millard and Bouillon 1975: 14. - Millard 1978: 197. - Gibbons and Ryland 1989: 414. - Calder 1991: 101. - Vervoort 1993: 214. - Hirohito 1995: 192. - Watson 1996: 78.

Sertularella sargassi Stechow, 1920, 37. - Stechow 1923: 179.

Sertularella quadrilateralis Hargitt, 1924: 493.

Sertularella diaphana var. *orthogona* Billard, 1925: 161. - Van Soest 1976: 83.

Sertularella diaphana var. *delicata* Billard, 1919, 21. - Billard 1925: 161.

Records and material. NTM C12912, alcohol preserved material; NTM C12972, MV F86922, microslides, colony from Stn 87. NTM C12914, alcohol preserved material NTM C12969, microslide, colony from Stn 154. NTM C12913, MV F86933, alcohol preserved material; NTM C12970, microslide, colony from Stn 110. Infertile branch fragments and small colonies. *Other records.* Stns 40, 113, 121, 131, 146, 156. East Point, Darwin, tall branched infertile colony, coll: J. E. Watson, depth 7 m, 11/8/1998. Plater Rock, large fertile colonies on coral boulders and *Eunice tubifex*, coll J. E. Watson, depth 3 m, 22/9/1999.

Description. Stems to 100 mm high, pinnately branched in one plane, lower stem thick, fascicled, polysiphonic tubes a continuation of hydrocladial filaments, stems becoming monosiphonic distally. Stem internodes short, broad, nodes transverse to slightly oblique, sometimes indistinct. Hydrocladia distal on cauline internodes, three hydrothecae on internode, one below hydrocladium, one in, or in front of axil and one opposite, axillar hydrothecae adnate to caulus and of same shape as others. Hydrocladia alternate, on indistinct apophysis, proximal part fairly long, slender, athecate, the first hydrotheca on basal side of hydrocladium.

Hydrothecae alternate, immersed in internode, short, widely separated laterally, base of each reaching about halfway up wall of that opposite, widest in proximal third, adcauline wall convexly curved, a small knot of perisarc at base, floor a downwardly tilted shelf, abcauline wall straight to slightly concave, contiguous with hydrotheca below. Margin subcircular in frontal view, tilted upwards at angle of 45° - 60° to hydrocladial axis, rim distinctly thickened with four equidistant, low rounded cusps, one abcauline, one adcauline and two lateral, separated by shallow embayments, no replication of margin, operculum of four fairly thick triangular flaps. Hydranth with deep abcauline caecum and about 20 tentacles.

Gonothecae borne on stem and hydrocladia, inserted without pedicel below a hydrotheca, a circular foramen connecting with hydrocladium; gonotheca elongate conical, adpressed to hydrocladium, perisarc thick, most with several longitudinal pleats, some indistinctly undulated.

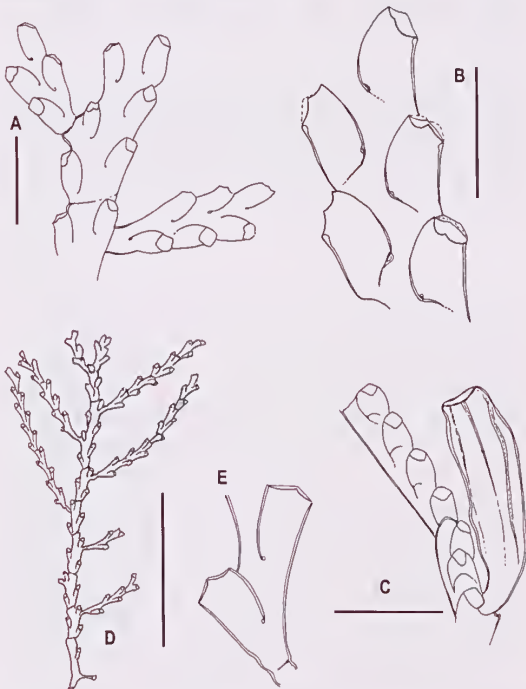


Fig. 24. *Sertularella diaphana*: A, hydrocladial part of stem from colony on *Eunice tubifex*. B, part of hydrocladial internode. C, gonotheca. D, colony corresponding to *Sertularella diaphana* var. *delicata* from *Gymnangium longirostre*. E, hydrothecae from same colony. Scale bars: A, E, 1,000 µm; B, D, 500 µm; C, 5,000 µm.

Colour. Live colonies orange to honey brown.

Measurements (μm).

Stem		
length of internode	900	- 112
diameter at node	460	- 600
Hydrocladium		
internode length	880	-1,700
diameter at node	160	- 200
width of apophysis	180	- 200
distance from apophysis to first hydrotheca	360	- 440
Hydrotheca		
length of adnate adcauline wall	360	- 392
length of free adcauline wall		48
diameter at margin	200	- 224
Gonotheca		
maximum length	2,060	-2,400
diameter at aperture	440	- 520

Remarks. Irregular transverse folds present in some gonothecae appear not to be normal ornamentation but are probably the result of interruptions or damage to growth.

A single, white, infertile stem 12 mm high, on *Gymnangium longirostre* from Stn 87, differs considerably from typical colonies of *Sertularella diaphana*. The slender, unfascicled stem has longer stem internode, greater separation of the hydrothecae along the hydrocladium, hydrothecae expanding to the margin and shorter adcauline wall (Figs 24C, D) conform exactly with *S. diaphana* var. *delicata* Billard, 1925. While concurring with Vervoort's (1993) rejection of the var. *delicata* as simply one of a range of intergrading forms of *S. diaphana*, it is possible that this variety may well be a distinct species. However, until the finding of a better range of fertile material the specimen is referred to *S. diaphana*.

Distribution. Virtually circumglobal in tropical and subtropical waters (Vervoort 1993). Tropical east and north-west Australia (Pennycuik 1959, Watson 1996).

Sertularella pinnata (Lamouroux, 1816)

(Fig. 25 A, B)

Caberea pinnata Lamouroux, 1816: 130.

Thuiaria lata Bale, 1882: 26. - Bale 1884: 120. - Bale 1894: 103. - Bale 1915: 287.

Sertularella lata - Nutting, 1904: 85. - Nutting 1905: 948. - Stechow 1913: 137. - Stechow 1923: 14. - Bale 1919: 337. - Jarvis 1922: 342. - Blackburn 1942: 115.

Sertularella tridentata Jäderholm, 1917: 13.

Sertularella ?diaphana - Stechow 1924: 69. - Stechow 1925, 226.

Sertularella pinnata - Gordon *et al.* 1998: 413.

Description. The following description is from a microslide held in the collection of the Museum of Victoria, Melbourne (MV F58895), labelled *Thuiaria lata* Bale, 1884 "co-type", and thought to be probably

syntype (Stranks 1993) and specimens in author's collection consisting of a large fertile colonies from 1) Crawfish Rock, Western Port, Victoria, depth 15 m, coll: J. E. Watson 24/11/66, 2) Green Cape, New South Wales, depth 17 m, coll: J. E. Watson 14/2/73.

Stems up to 200 mm high, 5 mm thick at base, plumose, with several secondary and tertiary branches given off in the same or nearly the same plane; stem and lower branches heavily fascicled, ultimate branches monosiphonic. Monosiphonic branch internodes short, very wide, nodes oblique, tilted in opposite directions, hydrocladium arising a little more than halfway up internode; internode with three hydrothecae, one in axil of hydrocladium, one below and one opposite.

Hydrocladia alternate on a short apophysis marked by a constriction in perisarc, hydrocladial internodes variable in length, two to five hydrothecae along each side, nodes distinct, oblique. Hydrothecae seated on front of hydrocladium, separated laterally, abcauline wall slightly sinuous, hydrotheca widest about middle, adcauline wall convex, completely adnate to internode; length-width ratio of abcauline to adcauline wall 1: 1.2; hydrotheca without true floor, a short spur of perisarc extending inwards from base of adcauline wall. Margin tilted upward at an angle of 55° - 60° to hydrocladial axis, circular in frontal view, with four low equidistant cusps, one abcauline, one adcauline and two lateral; rim thickened, margin not replicated, operculum of four flaps.

Gonotheca large, elongate conical, one to several along hydrocladium inserted without pedicel at base of a hydrotheca, connection with hydrocladium a wide foramen, gonotheca adpressed to or laying close to

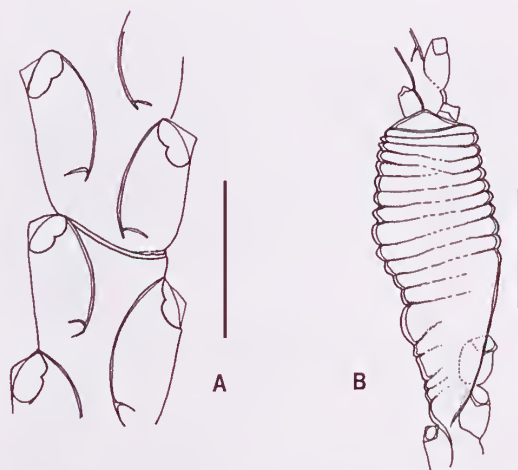


Fig. 25. *Sertularella pinnata*: A, hydrocladial internode. B, gonotheca. Scale bars: A, 500 μm ; B, 1,000 μm .

hydrocladium, perisarc thick with up to 14 smooth, deep transverse corrugations; corrugations less distinct on adcauline side and fading out proximally; orifice a shallow, circular apical depression, transverse to slightly oblique with a short adcauline lip; operculum a single thick flap.

Colour. Live colonies deep yellow to orange.

Measurements (μm).

Stem		
Length of internode	740	- 900
width at node	540	- 600
Hydrocladium		
length of internode	1,720	-2,100
width at node	360	- 400
width at apophysis	240	- 300
distance to first hydrotheca (proximal side)	140	- 200
Hydrotheca (hydrocladium)		
length adcauline wall	456	- 464
length abcauline wall	376	- 456
maximum width	216	- 240
diameter at margin	160	- 192
Gonotheca		
length	2,700	-2,840
width at aperture	820	-1,000

Remarks. The difficulty of distinguishing infertile material of *Sertularella pinnata* from *Sertularella diaphana* and other members of the group has been discussed by previous authors (e.g. Bale 1919, Gordon *et al.*, 1998). Bale considered the hydrothecae of *S. pinnata* to be "closer together, less laterally divergent, do not face as much to the front of the hydrocladium and the hydrothecal margins are more nearly vertical than those of *S. diaphana*". Some of these supposed differences may, however, be due as much to the angle of presentation of the specimen on the microslide as to actual orientation of the hydrothecae on the hydrocladium.

Nutting (1904) considered the type of *Thuiaria hyalina* Allman, 1888 from the coast of Brazil to be conspecific with *Sertularella lata* (Bale, 1884). His figure of the type clearly depicts the slight convexity near the base of the hydrothecal abcauline wall typical of *S. pinnata*. Jarvis (1922) reported *S. pinnata* from several east African localities and although her description is brief and lacks figures, the transversely corrugated gonotheca with flattened distal end leaves little doubt that the species is *S. pinnata*. Stechow (1925) doubtfully assigned infertile material from Shark Bay, Western Australia to *S. diaphana*; the slight tumescence of the abcauline hydrothecal wall (Stechow's Fig. H, p. 227) suggests that the species is probably *S. pinnata*.

Distinction between species of the *Sertularella* species group. Infertile material of *Sertularella quadridens*, *Sertularella diaphana* and *Sertularella pinnata* cannot be easily distinguished on microscopic characters alone, a situation that has probably led to much

past misidentification of species. When fertile they are, however, readily separated, the gonothecae of *S. quadridens* (Fig. 23F) and *S. decipiens* (Fig. 22E) being more or less tubiform and ridged, that of *S. diaphana* is conical with longitudinal pleats (Fig. 24E) while that of *S. pinnata* is conical and transversely corrugated (Fig. 25 B).

Ecology. In southern Australia, the large, plumose orange-yellow colonies of *Sertularella pinnata* usually grow in association with colonies of *Plumularia procumbens* Spencer, 1891 or rarely, epilithically (J. E. W., unpubl.). The tall, orange-coloured colonies are unmistakable and cannot be confused with any other southern Australian species.

As far as presently known all four species are epizooites, the tropical ones occurring chiefly on tubes of the polychaete *Eunice tubifex* while *Sertularella pinnata* is a virtual obligate on another hydroid.

Distribution. Southern Australia (Bale 1884, 1915; Jäderholm 1920; Gordon *et al.*, 1998), East Africa (Jarvis 1922) and Brazil (Nutting 1904).

Genus *Sertularia* Linnaeus, 1758 *Sertularia trigonostoma* Busk, 1852 (Fig. 26A-E)

Sertularia trigonostoma Busk, 1852: 387-392.
- Kirkpatrick 1890: 604. - Billard 1925: 174. - Pennycuik 1959: 198.

Sertularia trigonostoma var. *alternata* Vervoort, 1959: 284. - Mergner and Wedler 1977: 20.

Records and material. NTM C12903, alcohol preserved material; NTM C12951 microslide, colony from Stn 138. NTM C12904, alcohol preserved material; NTM C12899, MV F86924, microslides, colony from Stn 7. NTM C12905 alcohol preserved material, colony from Stn 82. Sparse, sparingly fertile colonies on pebbles and *Eunice tubifex*. *Other records.* Stns 84, 154.

Description. Hydorrhiza tubular, entwining substrate. Stems to 85 mm long, pinnate, lax, monosiphonic, cauline diameter decreasing distally, perisarc thick; proximal region of longer stems ahydrocladial, shorter stems entirely hydrocladial; cauline internodes indistinct.

Hydrocladia alternate, arising at an angle of c. 40° to cauline axis, longest in proximal stem region (up to 10 mm long on tallest stems), becoming shorter distally; hydrocladium inserted on long apophysis with distinct transverse distal node; two hydrothecae between each hydrocladium on same side, another in axil. Hydrocladial internode with two hydrothecae, node transverse to slightly oblique, distinct.

Hydrothecae biserial, subopposite, seated on front of internode, subopposite, slightly separated on proximal region of hydrocladium, adcauline walls adjoined distally along hydrocladium. Hydrotheca longer than wide, adcauline wall convex, free part very short, abcauline

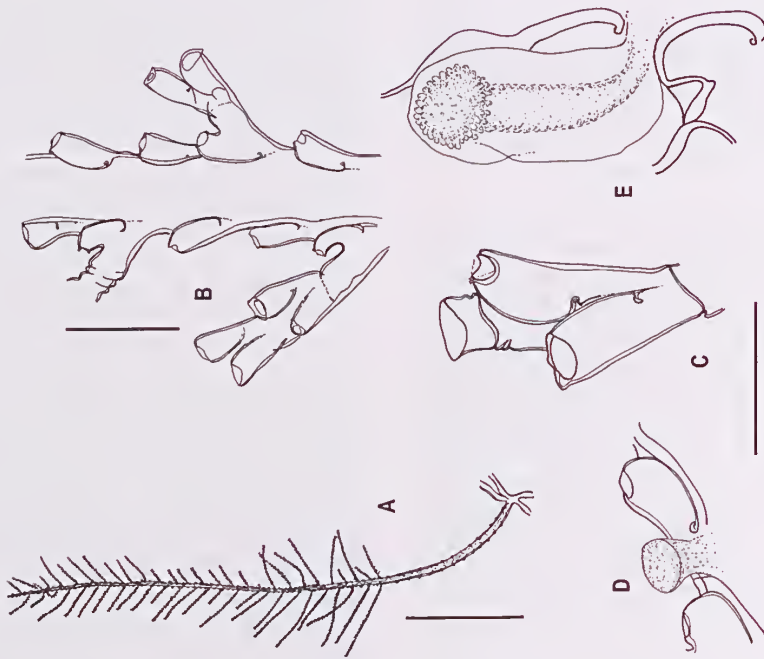


Fig. 26. *Serularella trigonostoma*: A, whole stem. B, hydrocladial part of stem. C, hydrocladial internode. D, developing gonotheca. E, immature gonotheca. Scale bars: A, 10 mm; B, 1,000 μ m; C, D, E, 500 μ m.

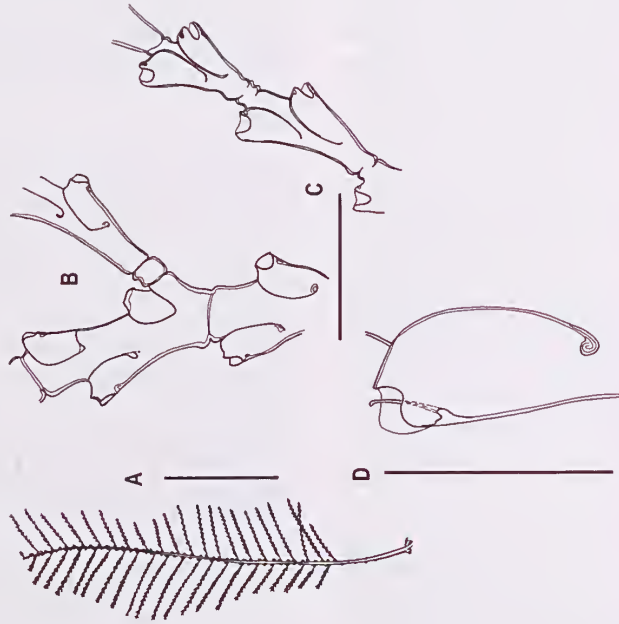


Fig. 27. *Thutaria operculata* sp. nov. A, stem from holotype from Darwin Harbour. B, part of stem of holotype with hydrocladium. C, hydrocladial internodes. D, hydrotheca with operculum. Scale bars: A, 10 mm; B, C, 500 μ m; D, 200 μ m.

wall straight to faintly sinuous or concave, contiguous with internode, base of adcauline wall with an inturred knot of perisarc, no true floor to hydrotheca, connection with hydrocladium wide. Margin thickened with two lobate lateral cusps and a much smaller adcauline cusp, aperture elliptical, opercular remnants obscuring most margins. Hydranths not well preserved, no caecum; approximately 16 tentacles.

Gonotheca immature, balloon-shaped to irregularly cylindrical, inserted without pedicel between two cauline hydrothecae in mid to upper stem region, expanding a little apically to a blunt distal end, gonophore an aborted hydranth, perisarc extremely thin.

Colour. Pale yellow-brown.

Measurements (μm).

Stem

distance between successive hydrocladia on same side	1,060 - 1,100
length of apophysis (distal side)	112 - 128
width of apophysis at distal node	144 - 160

Hydrocladium

length of internode	296 - 336
width at node	120 - 128

Hydrotheca

length of adnate adcauline wall	184 - 228
length of free adcauline wall (lateral view)	32 - 56
width between marginal cusps	88 - 112

Gonotheca

length	600
width	256

Remarks. Although the cauline perisarc is comparatively thick the stems are quite lax. Many hydrocladia are broken off at the distal apophysal node. The hydrothecal aperture is small and frequently obscured by adhering tissue and opercular remnants.

Vervoort (1959) erected the var. *alternata* to accommodate specimens from west Africa with alternate hydrothecae; the present material has subopposite hydrothecae, thus conforming to Busk's original description of the species.

This first description of the gonotheca is based on the single immature gonotheca present in the sample; it is remarkably small and delicate in comparison with the sturdy trophosome. As there is no sign of ova it is probably male.

Distribution. Tropical Indo-Pacific and Red Sea (Vervoort 1959, Mergner and Wedler 1977). Australian distribution: Torres Strait (Busk 1852) and tropical Queensland (Pennycuik 1959).

Genus *Thuiaria* Fleming, 1828

***Thuiaria operculata* sp. nov.**

(Fig. 27A-D)

Records and material. Holotype, NTM C12956, alcohol preserved material, NTM C12949, NTM

C12971, MV F86921, microslides from holotype colony, East Arm port, concrete wall of berth, coll: J. E. Watson, depth 5 m, 20/8/1998, colony of several infertile stems. Paratype, NTM C12973, microslide, two infertile stems on hydrorhiza of *Idiellana pristin*, Stn 146.

Description. Hydrorhiza thick, gnarled. Stems to 35 mm high, gracefully plumose, monosiphonic, proximal stem robust, perisarc thick, thinning distally, a distinct transverse node above base of stem, proximal cauline internode athecate, cauline and hydrocladial internodes thereafter thecate, nodes distinct to absent, slightly oblique to transverse, perisarc tumid above and below node.

Hydrocladium proximal on internode, a hydrotheca deep in axil, one above, margin almost level with distal node, another in alternate position, opposite on stem. Hydrocladia alternate, long, upwardly directed at 60 - 70° to cauline axis, borne on a strong apophysis with one or two transverse distal nodes, internodes thereafter with two hydrothecae, nodes slightly oblique.

Hydrothecae frontal on internode, subalternate, facing forward, adnate adcauline wall smoothly convex, free part short, a small hook-shaped knot of perisarc at base of wall; abcauline wall contiguous with internode, straight to slightly sinuous, maximum width of hydrotheca in distal third, a bracket-like internal submarginal shelf just below abcauline margin. Aperture oval, facing upward with two large lateral lobes and a very small adcauline cusp; operculum a strong flap with outrolled rim, attached to abcauline submarginal shelf; perisarc of operculum thick. Hydranth with c. 10 tentacles, abcauline caecum visible in some hydranths.

Colour. Live stems pale greenish-white.

Measurements (μm).

Stem

diameter of basal node	176 - 208
length of internodes	560 - 680
diameter at node	112 - 168

Branch

length of internode	400 - 520
diameter at node	72 - 96
abcauline length of apophysis from stem node	180 - 208
length of first athecate internode	60 - 72

Hydrotheca

length of adnate adcauline wall	180 - 204
length of free adcauline wall	32 - 44
maximum width	96 - 100

Remarks. The abcauline operculum of one valve and hydranth with abcauline caecum necessitates referral of the species to *Thuiaria*. The operculum attached to the knuckle-shaped submarginal shelf is quite delicate in frontal view but in lateral view appears much thicker, its outrolled upper edge being quite clear. In contracted hydranths the small abcauline caecum is rather obscure, being evident in extended hydranths.

Etymology. Named for the strongly developed opercular flap.

***Thuiaria plumularioides* sp. nov.**

(Fig. 28A-F)

Records and material. Holotype, NTM C12974, NTM C12975, MV F86923, microslides, from infertile colony on sponge, Stn 153. Paratypes, NTM C12976, microslide, colony from Stn 110. NTM C12977, microslide, colony from Stn 154. (All holotype and paratype material mounted on microslides: no preserved material remaining).

Description. Hydromorpha a knot of tubes entwining substrate. Stems to 25 mm high, straight, robust, pinnate, proximal part of stem ahydrocladate but with two rows of opposite hydrothecae; ahydrocladate part of stem usually with a strong distal hinge joint. Cauline nodes of hydrocladate part of stem distinct, slightly oblique to transverse; internode with three hydrocladia, one to three hydrothecae above hydrocladium, proximal one axillar, distalmost level with node. Cauline perisarc very thick proximally, thinning a little distally.

Hydrocladia close set, alternate, long, arching gracefully upwards at an angle of c. 30° to cauline axis from a strong apophysis with an indistinct transverse constriction and a pronounced distal hinge joint. Hydrocladial internodes long, nodes distinct hinge joints. Hydrothecae biserial, frontal on hydrocladium, proximal internodes bearing up to 10 pairs of hydrothecae, pairs becoming fewer distally; hydrothecae overlapping,

facing upwards, sub-opposite on proximal region of hydrocladium, becoming opposite distally, each pair overlapping base of pair above. Hydrotheca long, tubular (lateral view), almost vasiform (anterior view), slightly tumid at base, narrowing just behind margin, adcauline walls joined, straight, a short convex length free of internode at a sharp outward distal bend; abcauline wall almost straight, a prominent abcauline submarginal shelf, a foramen at base of wall connecting with internode, base of hydrotheca rounded. Aperture oval, margin thickened with a pair of opposite laterally placed cusps and a rounded adcauline lobe; opercular valve attached to submarginal adcauline shelf. Hydranth with an abcauline caecum and about 10 tentacles.

Colour. In life, pale yellow.

Measurements (µm).

Stem

maximum diameter at proximal node	850
length of internode	960 - 1,960
diameter at node	220 - 500
apophysis, length of abcauline wall	280 - 360
apophysis, width at transverse node	144 - 184

Hydrotheca

length of adnate adcauline wall	184 - 240
length of free adcauline wall to margin	100 - 160
length of abcauline wall to top of margin	240 - 280
depth of margin, lateral view	60 - 64
width of margin, cusp to cusp, frontal view	68 - 80

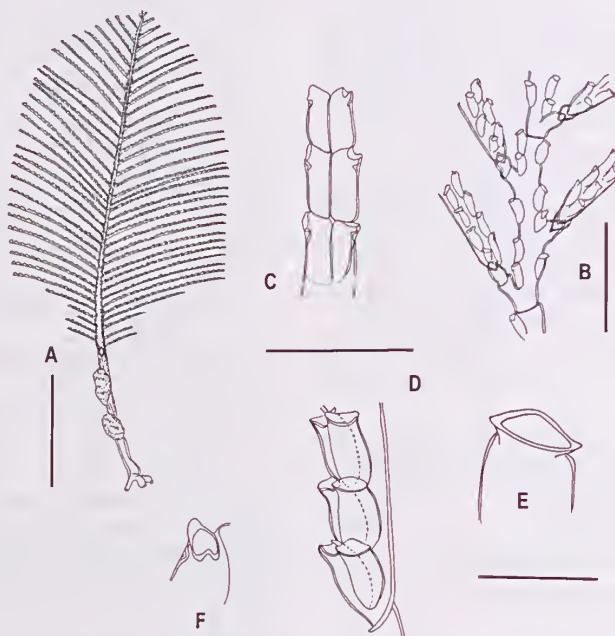


Fig. 28. *Thuiaria plumularioides* sp. nov. A, stem from holotype colony. B, hydrocladia. C, frontal view of hydrocladium. D, hydrocladium, lateral view. E, hydrotheca showing lobate margin. F, lateral view of hydrotheca showing submarginal abcauline thickening. Scale bars: A, 10 mm; B, 1,000 µm; C, D, 500 µm; E, F, 200 µm.

Remarks. The species is referred to *Thuiaria* on the basis of the abcauline caecum in the hydranth and the hydrotheca having an abcauline operculum. Colonies may be sparingly branched, one stem of the holotype colony having remnants of a branch near the base. The overlapping hydrothecae and slightly tumid base of the hydrothecae are characteristic.

Etymology. The species is named for its plumose morphology.

Genus *Thyroscyphus* Allman, 1877

Thyroscyphus macrocytharus (Lamouroux, 1824) (Fig. 29A)

Clytia macrocytharus Lamouroux, 1824: 647.
- Lamarek 1837: 199.

Campanularia marginata Bale, 1884: 54. - Bale 1888: 758. - Bartlett 1907: 62. - Levinsen 1913: 289.

Laomedea marginata - von Lendenfeld 1885a: 404.

Thyroscyphus marginatus - Bale 1914: 91. - Bale 1915: 245, 258. - Stechow 1924: 69. - Stechow 1925: 217. - Blackburn 1942: 112. - Watson 1973: 169.

Thyroscyphus balei Calder, 1983: 16. - Watson 1992: 220.

Thyroscyphus macrocytharus - Watson 1994: 156.
- Watson 1996: 78. - Watson 1997: 517.

Record and material. NTM C12987, MV F86893, microslides, sparingly fertile colony of four straggling stems on sponge, Stn 154.

Description. Hydorhiza reptant on substrate, hydrocaulus of same diameter as hydorhiza, monosiphonic, perisarc very thick. Stems to 10 mm high, internodes long, smooth, almost geniculate, nodes oblique, deeply incised. Hydrothecae alternate, distal on internode, borne on a moderately long pedicel either smooth or with one or two constrictions; hydrotheca campanulate, margin quadrate, conspicuously thickened, with four pointed cusps and four shallow emarginations; operculum of four equal valves. Gonotheca immature, top-shaped, borne on a short pedicel inserted in apophysis of stem beside hydrotheca.

Colour. Pale brown to colourless.

Measurements (µm).

Stem	
length of internode	960 - 1,320
width at node	168 - 256
Hydrotheca	
length of pedicel	100 - 240
depth, diaphragm to margin	680 - 792
diameter at margin	528 - 568

Remarks. The specimen conforms to the description of *Thyroscyphus macrocytharus* given by Watson (1994). Most hydrothecal pedicels of the present material are regenerated, some up to eight times. *Thyroscyphus macrocytharus* is endemic to Australia, usually occurring in shallow water; the present record from a depth of 30 m is the second deepest record for the species, the deepest being 137 m off southern Australia (Bale 1915).

Distribution. The previous northernmost record of *T. macrocytharus* is from Geraldton, Western Australia (Stechow 1925). This is the first record of the species from tropical Australia.

Thyroscyphus torresii (Busk, 1852) (Fig. 29B-C)

Laomedea torresii Busk, 1852: 402.

Thyroscyphus simplex Allman, 1888: 25. - Jäderholm 1903: 273. - Jäderholm 1916: 5. - Stechow and Müller, 1923: 466.

Campanularia torresii - Bale 1884: 52. - Kirkpatrick 1890: 604.

Thyroscyphus regularis Jäderholm, 1896: 9.

Thyroscyphus torresii - Jäderholm 1903: 273. - Stechow 1913: 12. - Jäderholm 1916: 5. - Stechow and Müller 1923: 466. - Redier 1963: 22. - Watson 1996: 78.

Cnidocyphus torresii - Splettstösser 1929: 70-82, 125. - Pennycuik 1959: 156. - Vervoort 1941: 204. - Vervoort 1993: 104.

Records and material. NTM C12887, alcohol preserved material, colony from Stn 110. NTM C12886 alcohol preserved material; NTM C12989, MV F86892, microslides, colony from Stn 13. NTM C12888, alcohol preserved material, colony from Stn 136. MV F86938, alcohol preserved material, colony from Stn 137. NTM C12988, microslide, colony from Stn 138. Many infertile colonies, the largest of 20 stems on shell and grit, *Gynnaugium longicorne* and sponge. **Other records.** Stns 48, 67, 78, 87, 127, 136, 155. East Port channel and wharf pilings, small and large colonies, Port of Darwin, coll: J. E. Watson, depth 3 m, 16/8/1998. Plater Rock, many sparsely fertile large and small colonies, coll J. E. Watson, depth 3 - 10 m, 21/9/1999.

Description. Hydorhizal stolons tightly entwining substrate. Clusters of up to 20 pinnate stems to 100 mm high arising from hydorhiza, basal stem region lightly fasciated by hydorhizal stolons, stems thereafter monosiphonic, tubular, stiff and robust, perisarc of basal region very thick and smooth, thinning distally. Hydrocladia pinnate, alternate, well separated, long, no secondary branching, two alternate hydrothecae on stem between each branch and one axillar. Stem and hydrocladial internodes fairly long, nodes slightly oblique to transverse, marked by a notch in perisarc. Hydrocladial apophysis long, inclined upwards, proximal side marked by an indentation in perisarc in stem; first hydrocladial internode long, internodes shorter thereafter, nodes transverse, usually distinct.

Hydrothecae alternate, pedicel short, thick, smooth or with several ridges; hydrotheca asymmetrical, abcauline wall straight, proximal third of abcauline wall convex, the curve straightening out distally, diaphragm distinct, down-curved, often asymmetrically tilted, hydrothecal margin circular, rim quadrate with four low,

equidistant, sharply pointed cusps separated by four shallow emarginations; operculum thin, of four triangular flaps. Hydranths stubby, with at least 30 tentacles.

Gonothecae immature, top-shaped, arising in proximal stem region beside a hydrotheca or on stem, hydrocladium or apophysis from which a hydrotheca has been shed; perisarc thin.

Colour. Live colonies golden-yellow to golden-brown.

Measurements (µm).

Stem		
diameter at base	860	- 950
distance between successive branches	2,300	-2,800
length stem internodes between successive hydrothecae	800	-1,000
Branch		
length first internode	1,900	-2,040
length succeeding internodes	700	-1,100
width branch at base	200	- 260
width at node	192	- 224
Hydrotheca		
length, including pedicel	1,080	-1,200
length of pedicel apophysis to diaphragm	120	- 152
width of pedicel	160	- 192
width at diaphragm	240	- 280
diameter at margin	472	- 576
width of marginal embayment	232	- 320

Remarks. The hydrothecal pedicels of younger hydrocladia are usually smooth but in older stems are often ridged from repeated breakage and regeneration. There is no submarginal thickening of the hydrothecal rim as in *Thyroscyphus macrocytharus*, only a faint line below the rim in some hydrothecae marking the junction of the operculum with the body. Several colonies are infested with *Hebelopsis scandens*, the hydrothecae of which are invariably close beside those of *Thyroscyphus*.

The lower stem regions bearing developing gonothecae are packed with globular white bodies, apparently developing gonophores which are visible through the stem perisarc. It is surprising that, as *T. torresii* is one of the most abundant hydroids in both dredged and scuba collections, only a few immature gonothecae were found. The only description and figure of the mature gonotheca of *T. torresii* is of a distally ridged gonotheca (Jäderholm 1903).

Distribution. Indonesia, China Sea, Mergui Archipelago (Vervoort 1993). Australian region: Torres Strait (Busk 1852, Kirkpartick 1890) Aru Sea (Stechow and Müller 1923), Fitzroy Island (Bale 1884), off Cape York (Allman 1888), Cape Jaubert, Western Australia (Jäderholm 1916), Queensland (Pennycuik, 1959).

***Thyroscyphus fruticosus* (Esper, 1793)**

(Fig. 29D)

Spongia fruticosus Esper, 1793: 188.

Sertularella fruticosus - Thompson 1879: 100.

Campanularia fruticosus - Marktanner-Turneretscher 1890: 205.

Thyroscyphus vitiensis Marktanner-Turneretscher, 1890: 210. - Billard 1907: 343. - Jarvis 1922: 338.

Lytoscyphus fruticosus - Bedot 1905: 51. - Stechow and Müller 1923: 465. - Stechow 1925: 215.

Thyroscyphus fruticosus - Splittstösser 1929: 7, 122. - Billard 1933: 11. - Vervoort 1941: 202. - Vervoort 1946: 306. - Millard 1952: 199. - Ralph 1961: 754. - Vervoort 1965: 35. - Vervoort 1967: 35. - Schmidt 1971: 35. - Millard and Bouillon 1973: 76. - Millard 1975: 323. - Mergner and Wedler 1977: 18. - Gibbons and Ryland 1989: 425. - Watson 1996: 78.

Record and material. NTM C12889, MV F86945, alcohol preserved material; NTM C12990, microslide, Plater Rock, tall colonies on coral boulders and rock, coll: J. E. Watson, depth 5-8 m, 22/9/1999.

Description. Colonies of up to 10 stems to 150 mm high. Hydrorhiza a tangled mass of tough tubes embedded in substrate. Stem and branches stiff, monosiphonic, proximal part of stem athecate; branching irregular, predominantly in one plane, usually almost perpendicular to stem, no division into nodes, tubular in section, each segment widening to a short, proximally swollen apophysis supporting a hydrotheca. Perisarc of stem and branches very thick and smooth.

Hydrothecae strictly alternate on opposite sides of stem and branches, one in axil of branch; hydrotheca inclined upwards on a short thick pedicel, smooth or with one or two constrictions, tubular, asymmetrical, abcauline wall straight, adcauline wall convex, widest at proximal third, both walls narrowing slightly but distinctly behind margin; diaphragm distinct, marked by a circular shelf in perisarc tilted obliquely downwards; margin circular, rim thickened, an internal band of tissue below margin at narrowest point of hydrothecal body, margin sometimes with four almost imperceptible equidistant cusps, sometimes with one or two renovations. Operculum delicate, of four equal triangular valves.

Gonothecae borne on a short, thick pedicel below hydrothecal apophyses on stem and branches, larger than hydrotheca, top-shaped, tilted downwards, perisarc thick, smooth to rather lumpy, distal end obliquely truncated, sealed by a plug of tissue. Gonophore (possibly female) distal in gonothecal cavity.

Colour. Stem and branches of live colonies honey brown, hydrothecae and gonothecae rose pink; colony yellow-brown when preserved.

Measurements (µm).

Stem and branches		
diameter above hydrothecal pedicel	340	- 380
distance between successive hydrothecae on same side	1,480	-2,900
width below apophysis	400	- 540

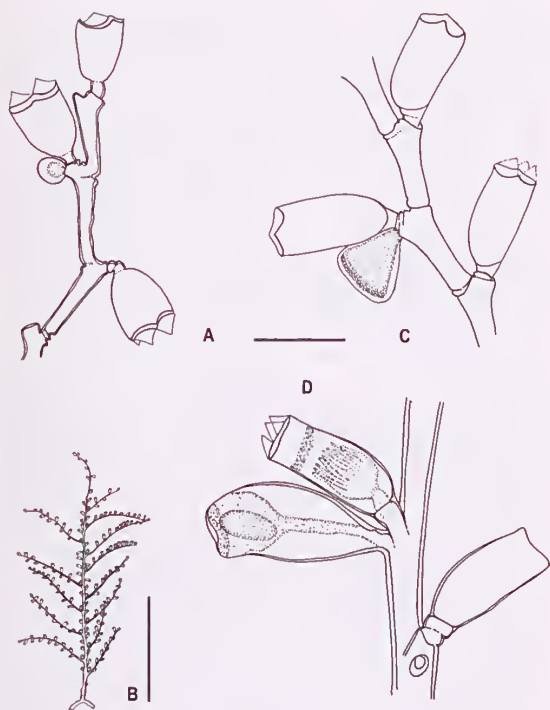


Fig. 29. A, *Thyroscyphus macrocytharus*: part of stem with developing gonotheca. B, C, *Thyroscyphus torresii*: B, fertile colony from Plater Rock. C, branch internodes with hydrothecae and young gonotheca. D, *Thyroscyphus fruticosus*: internodes from fertile colony from Plater Rock. Scale bars: A, C, D, 1,000 µm; B, 5,000 µm.

width across distal node of apophysis	240 - 320
Hydrotheca	
length (diagonal) of adcauline wall, diaphragm to margin	1,300 - 1,500
length of abcauline wall, diaphragm to margin	1,140 - 1,200
diameter of margin	488 - 536
length (abcauline side) of pedicel, apophysis to diaphragm	280 - 320
width of pedicel above apophysis	208 - 240
Gonotheca	
length	1,460 - 1,760
maximum width	840 - 940
diameter at margin	640 - 720

Remarks. *Thyroscyphus fruticosus* and *T. torresii* from the Beagle Gulf and Darwin share many characters, particularly in size of colony, habit and choice of habitat. The only reliable means of distinguishing between the species *in situ* is in the slightly more straggling colonies and pink colour of *T. fruticosus* while *T. torresii* is tidier in aspect and is honey brown in colour. Gibbons and Ryland (1989) reported very short (10 - 40 mm high) violet-coloured colonies of *T. fruticosus* from rock and sandy habitats in Fiji. The pink colouration of *T.*

fruticosus is lost in preservation, a reaction also noted by Millard (1975).

Confusing morphological similarities of *T. fruticosus* with *T. torresii* have probably led to some past confusion of the species, for example Gibbons and Ryland (1989, fig. 40) depict asymmetrical hydrothecae, clearly those of *T. fruticosus*, but with marginal cusps more resembling those of *T. torresii*. In sterile material, the only reasonably constant morphological differences are the absence of internodes from stem and branches of *T. fruticosus*, the usually larger hydrothecae and the sometimes almost imperceptible narrowing of the adcauline wall behind the margin.

Distribution. Mediterranean Sea, Indo-West Pacific Timor Sea, New Zealand. Australian distribution, north-western Australia (Watson 1996).

Family Syntheciidae Marktanner-Turneretscher, 1890 Genus *Synthecium* Allman, 1872

Diagnosis. Colony with erect stem bearing hydrocladia in opposite pairs. Stem and hydrocladia bearing hydrothecae in opposite pairs, the pairs always in the same plane forming two longitudinal rows. Gonothecae dioecious, springing from within hydrothecae.

Remarks. Seven species of *Synthecium* are reported from Australia: *Synthecium patulum* (Busk, 1852), *Synthecium orthogonium* (Busk, 1852), *Synthecium elegans* Allman, 1872 (see Jäderholm 1917), *Synthecium campylocarpum* Allman 1888, *Synthecium subventricosum* Bale, 1914 (recognised by Ralph (1958) as a small form of *Synthecium elegans*), *Synthecium megalothecum* Billard, 1924 (see Pennycuik 1959) and *Synthecium dentigerum* Jarvis, 1922 (see Watson 1969).

Even with fertile material it can be difficult to differentiate between species of *Synthecium*. Size differences between hydrothecae in male and female colonies reported in some species, are a further complicating factor. *Synthecium orthogonium* and *Synthecium campylocarpum* have been confused in the past and as no type material of *Synthecium patulum* is known to exist (see Totton 1930) concepts of the species have varied widely. Bale (1888) reported *Synthecium orthogonium* (here considered to be *S. campylocarpum*, see discussion later) from off the coast of New South Wales and Billard (1925) synonymised *S. orthogonium* and *S. campylocarpum* in *S. patulum*. *Synthecium orthogonium* from Indonesia was identified by Vervoort (1941) as *S. patulum* while the description and figure of a gonotheca identified as *S. patulum* by Millard and Bouillon (1973, 1975) is clearly that of *S. campylocarpum*.

The Beagle Gulf and Darwin collection includes two species, the most abundant of which is *Synthecium campylocarpum*; the other, less common, is here referred to *Synthecium orthogonium*. Although *Synthecium patulum* is not represented in the present collection, the

identity of other species rests largely upon establishment of the true identity of *S. patulum*. For comparison, a redescription of *S. patulum* from southern Australia is given, based on extensive material in the author's collection and holdings in the collection of the Museum of Victoria.

***Synthecium campylocarpum* Allman, 1888**
(Figs 30A-G, 31A-C)

Synthecium campylocarpum Allman, 1888: 78.
- Marktanner-Turneretscher 1890: 248. - Inaba 1890: 52-54. - Farquhar 1896: 466. - Stechow 1913: 127.
- Jäderholm 1919: 14. - Totton 1930: 169. - Ralph 1958: 347. - Yamada 1959: 52. - Hirohito 1969: 18. - Watson 1996: 78.

Synthecium orthogonium (Busk, 1852). - Bale 1888: 767. - Bale 1924: 250.

Records and material. NTM C12933, MV F86946, alcohol preserved material; NTM C12979, MV F86097, microslides, colony from Stn 111. NTM C12980, NTM C12981, microslides, colony from Stn 20. NTM C12983, microslide, colony from Stn 13. NTM C12934, NTM C12935 alcohol preserved material, colony from Stn 81. Colonies in poor condition on digitate sponges and *Eunice tubifex*, Plater Rock, large male colony on digitate sponge, coll J. E. Watson, depth 5 m, 22/9/1999. East Arm channel, large male colonies on *Eunice tubifex*, coll J. E. Watson, depth 3 m, 17/8/1998. **Other records.** Stns 21, 110, 26.

Description. Stems to 100 mm high. Hydrorhiza tubular, reptant on host, perisarc of hydrorhiza and stems thick. Stems wide proximally, narrowing distally, proximal internodes usually athecate, internodes thereafter long with one to three pairs of distal hydrothecae; hydrocladia opposite, distal on internode, given off at an angle of 60° - 90° to caulus above cauline hydrothecal pair; nodes transverse, distinct in younger parts of stems, indistinct to completely absent from older parts, sometimes a secondary node between primary nodes. Hydrocladia on a long vasiform apophysis, sometimes a transverse distal node below first hydrothecal pair. Hydrothecae opposite, occupying almost or entire internode, nodes vestigial or absent, hydrothecae often in contact vertically, a little separated in front, in contact behind; hydrotheca tubular, adcauline wall smoothly convex, one fifth to one quarter of wall free of internode, abcauline wall straight or slightly tumescent proximally, becoming concave, curvature increasing distally, perisarc thinning a little towards margin. Margin circular, sinuous, facing slightly forward, parallel to hydrocladial axis or tilted slightly upward, rim outrolled, sometimes up to four renovations from within hydrotheca.

Colonies dioecious, gonothecae borne on lower stem and hydrocladia. Male gonotheca long, irregularly pod-shaped, usually widest about middle, pedicel inserted

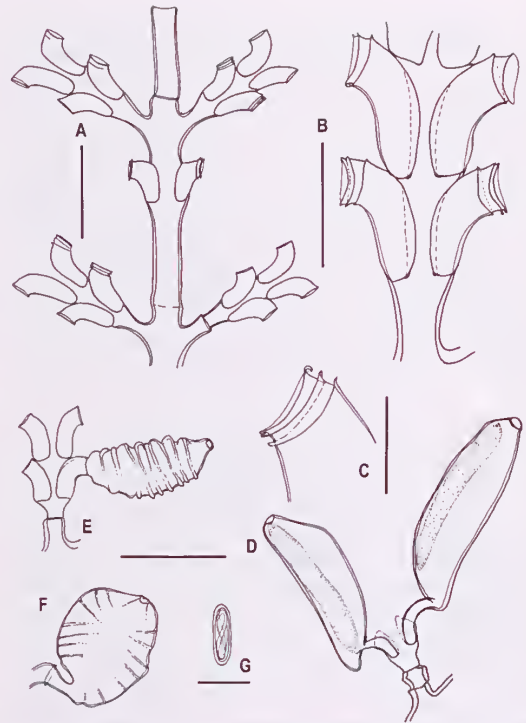


Fig. 30. *Synthecium campylocarpum* from Beagle Gulf and Plater Rock: A, hydrocladial part of stem. B, hydrocladial internode. C, hydrotheca with everted marginal replications. D, male gonotheca. E, lateral view of female gonotheca. F, frontal view of female gonotheca. G, nematocyst (haploneme?) from hydrocaulus. Scale bars: A, B, 500 µm; C, 200 µm; D - F, 1,000 µm; G, 50 µm.

with a right-angled bend deep into hydrotheca, often splitting hydrotheca; perisarc of gonotheca rather thin, smooth to faintly undulated, orifice small, circular, operculum a thin sheet of tissue, gonophore elongate. Female gonotheca small, lenticular, one side usually flat, other side convex, perisarc thicker than male, six to eight transverse ribs crossing entire body, more deeply incised on flatter side, ribs fading out proximally and distally, orifice small, circular, on a short tubular neck, neck foreshortening as gonotheca matures.

Cnidome of large ?haplonemes with blunt ends, capsule 62.5 x 17.5 µm, tubule coiled, in tentacles and coenosarc of stems.

Colour. Live colonies yellow; female gonophore orange.

Measurements (µm).

Hydrorhiza	
diameter	350 - 450
Stem	
length of internode	
(distance between hydrocladia)	1,700 - 2,000
diameter at node	240 - 320
Hydrocladium	
maximum length	8,000

length of apophysis to first hydrothecal pair	216 - 280
width across base of hydrothecal pair	296 - 336
Hydrotheca	
length of adnate adcauline wall	448 - 480
length of free adcauline wall	96 - 168
length of abcauline wall	256 - 368
diameter of margin	184 - 208
Gonotheca	
length of mature male	1,820 - 2,200
maximum width of male	560 - 700
length of mature female	1,120 - 1,600
width of female, frontal view	940 - 1,100
width of female, side view	640 - 740

Remarks. Apical tendrils occur on several of the longer stems. On some older stems, hydrocladial apophyses are regenerated up to three times, each regrowth marked by a shoulder-like node. The large range of material examined revealed no difference in height of stems nor in size of hydrothecae between sexes.

Bale (1888) referred to *S. orthogonium* a specimen from Port Jackson, on the eastern Australian coast, later finding nothing (Bale 1914, 1924) to distinguish it from *S. campylocarpum*. His opinion was followed by many later authors (c.g. Thornely 1904, Nutting 1905, Jäderholm 1903, Jäderholm 1916, Stechow and Müller 1923), none of whom described or figured their specimens. Ritchie (1911) assigned specimens from the eastern Australian coast to *S. orthogonium* noting that their dimensions did not agree very well with Billard's (1910) measurements of the holotype of that species. His description of the hydrotheca with sinuate margin is undoubtedly of *S. campylocarpum*.

I have compared a microslide preparation of a syntype of *Syntheicum campylocarpum* from the *Challenger* collection, taken off the eastern Australian coast (Museum of Victoria collection registered number MV F58214), with a microslide specimen identified by Bale (1888) as *S. orthogonium* (specimen also held in the Museum of Victoria). The *Challenger* material is an almost complete fertile stem with young male gonothecae (Fig. 31D-F) and is almost identical with Bale's specimen, thus supporting Ralph's (1958) view that Bale's specimen is not *S. orthogonium* but *S. campylocarpum*.

When examined in isolation infertile material of *S. orthogonium* may be confused with *S. campylocarpum*, especially in colonies of *S. campylocarpum* in which the hydrothecae are more outwardly bent than usual. They are best distinguished by the larger and more robust stems and distinctly sinuate margin of *S. campylocarpum* compared with the smaller, more delicate stems and sharply bent hydrotheca without marginal sinuosity of *S. orthogonium*.

Distribution. Known from eastern subtropical to tropical northern Australia (Watson 1996) New Zealand, (Ralph 1958) Japan (Hirohito 1969).

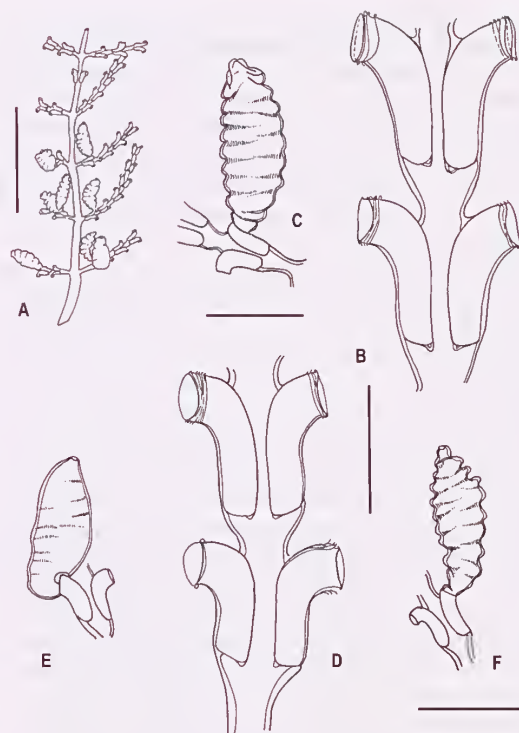


Fig. 31. *Syntheicum campylocarpum*, syntype, from Port Jackson, *Challenger* Expedition. MV F58214: A, part of fertile stem. B, hydrocladial internode, hydrothecae with replicated margin with outrolled rim. C, male gonotheca. D, hydrocladial internode from a microslide specimen from Port Jackson, identified by Bale (1888), as *Syntheicum orthogonium* held in Museum of Victoria. E, male gonotheca from same specimen. F, female gonotheca from same specimen. Scale bars: A, 5,000 μ m; B, D, 500 μ m; C, E, F, 1,000 μ m.

Syntheicum orthogonium (Busk, 1852)
(Fig. 32A-F, Table 4)

Sertularia orthogonia Busk, 1852: 390. - Bale 1884: 88. - Billard 1910: 25.

Not *Syntheicum orthogonium* - Bale 1888: 767. - Bale 1924: 250.

?*Syntheicum orthogonium* - Jäderholm 1903: 289. - Jäderholm 1916: 6. - Thornely 1904: 119. - Nutting 1905: 950. - Stechow and Müller 1923: 465. - Pennycuik 1959: 190. - Watson 1996: 78.

Syntheicum patulum (Busk, 1852) - Billard 1925: 125. - Vervoort 1941: 199.

Records and material. NTM C12936, alcohol preserved material, colony from Stn 136. NTM C12984, NTM C12985, MV F86890, microslides, infertile sparse colony on *Gymnangium longicorne* from Stn 87. NTM C12986, microslide, small fertile colony on aglaopheniid hydroid, Plater Rock, coll: J. E. Watson, depth 4 m, 21/9/1999.

Description. Hydorrhiza tubular, reptant; stems short, to 35 mm high, lax, tubular, with two or three pairs of opposite hydrocladia, proximal stem region athecate, variable in length; diameter of stem diminishing and thickness of perisarc reducing distally; stem internodes long, nodes when present, a transverse constriction in perisarc; one or two pairs of hydrothecae about halfway to two thirds up internode; hydrocladia long and flexuous, opposite or single, given off at a slight upward angle from a strong shoulder-like apophysis.

Hydrocladial nodes marked by a pronounced narrowing of perisarc or a transverse line, hydrothecae paired, distal on internode, proximal pair displaced slightly relative to one another; hydrothecae long, tubular, pairs may or may not be conjoined, adnate adcauline wall almost straight to faintly convex, free part bending sharply outwards and slightly forward perpendicular to hydrocladial axis for one third to half adcauline length, sometimes an internal thickening of perisarc at junction of adnate and free wall; abcauline wall slightly tumescent above base, almost straight to distal bend, then either straight or concave to margin, often an internal thickening of wall in bend. Margin parallel or almost parallel to hydrocladial axis, circular, rim strongly everted, some with up to seven marginal replications; perisarc of hydrotheca smooth.

Gonotheca on a short pedicel issuing from a hydrotheca in lower stem region, gonotheca sausage-shaped, tapering distally, body with two rows of 10 deep corrugations along one side, corrugations smoothing out behind; distal end obtuse, no orifice evident.

Colour. Live colony mauve, white or colourless when preserved.

Comparison of Beagle Gulf specimens with holotype. I have compared specimens from the Beagle Gulf and Darwin Harbour with the holotype of *Synthecium orthogonium* (Busk, 1852) from the type locality of Torres Strait, loaned by the Natural History Museum, London (Fig. 32 E, F). The NHM microslide preparation labelled "*Sertularia orthogonia* Australia, Rattles, Holotype, Busk 1852, Busk Coll: 99. 7. 1. 6367" consists of two stem fragments, one 7 mm long and the other 5 mm long, in good condition but without hydorrhiza. There are several pairs of opposite hydrocladia, one pair per internode, given off from just below a node. The hydrocladia bear up to seven pairs of opposite hydrothecae, one pair per internode; adcauline walls of some pairs joined but others separated. Hydrothecae tubular, distal on internode and sharply bent outwards below node where adcauline wall becomes free. Margin circular and parallel to hydrocladial axis; margins of several hydrothecae are sufficiently well preserved to show replication of the rim. Internal thickening of the abcauline wall is minimal, probably due to shrinkage over time. The Beagle Gulf and Darwin specimens almost exactly conform with the type, the only difference being

the somewhat shorter stem internodes, a variable character of little diagnostic value in the genus. Dimensions of the Beagle Gulf and Darwin specimens are compared in Table 4 with those of the holotype of *S. orthogonium*.

Busk (1852) considered that the strong outward bend of the hydrotheca of *Synthecium orthogonium* clearly characterised the species but later speculated that *S. orthogonium* may be a variety of *Synthecium patulum* (Busk, 1852) from southern Australia. Bale (1884) reported and figured *S. patulum* from Port Phillip Bay in southern Australia but did not comment upon any supposed relationship with *S. orthogonium*, continuing to regard *S. patulum* a distinct species (Bale 1914a). Billard (1925) described and accurately figured *S. orthogonium* and its gonangium from Indonesia but, like many other authors, assigned it to *S. patulum*. Comparison of dimensions tabulated above and dimensions (Figs 32, 33) show that the free adcauline wall of *S. orthogonium* is much longer and the hydrothecal margin much narrower than that of *S. patulum*. Fresh material of *S. orthogonium* is readily distinguishable from *S. patulum*, colonies of *S. orthogonium* being much smaller and more delicate than *S. patulum*. Although closely related, they are here regarded as distinct species.

Distribution. On present knowledge, *Synthecium orthogonium* is a tropical species the only reliable records of which are from Torres Strait (Busk 1852) and Indonesia (Billard, 1910).

Table 4. Comparison of measurements (μm) of Beagle Gulf and NHM Busk specimens of *Synthecium orthogonium*.

	Beagle Gulf, Darwin	NHM Busk specimen
Hydorrhiza diameter	112 - 200	-
Stem		
length of internode (distance between hydrocladia)	800 - 2,800	1,880 - 1,960
diameter at node	140 - 160	152 - 176
diameter lower stem	260	200
diameter thecate part of stem	216 - 264	184 - 224
Hydrocladium		
maximum length	4,000	-
length apophysis to first hydrothecal pair	108 - 272	-
width across base of first hydrothecal pair	256 - 320	-
Hydrotheca		
length of adnate adcauline wall	440 - 480	408 - 464
length of free adcauline wall	208 - 320	192 - 240
length of abcauline wall (diagonal)	360 - 440	328 - 376
length of abcauline wall base to bend	320 - 326	-
length of abcauline wall bend to margin	136 - 160	-
diameter of margin	136 - 160	120 - 152
length of outrolled rim	8 - 16	-
Gonotheca		
length	1,300 - 1,400	-
maximum width	360 - 376	-

Syntheicum patulum (Busk, 1852)

(Fig. 33A-G, Table 5)

Sertularia patula Busk, 1852, 390. - Bale 1884: 88.*Syntheicum patulum* - Bale 1888: 766. - Hodgson 1950:18. - Watson 1975: 165. - Watson 1994: 66.*?Syntheicum patulum* - Jarvis 1922: 332, 345. - Trebilcock 1928: 9. - Pennycuik 1959: 190.Not *Syntheicum patulum* - Billard 1925: 125. - Vervoort 1941:199. - Millard and Bouillon 1973: 64. - Millard 1975: 12. - Vervoort 1987: 94.

Description. Stems up to 50 mm high, occasionally with secondary branching; hydrorhiza tubular, reptant, perisarc of stems and hydrocladia fairly thick. Proximal ahydrocladial stem segment variable in length, some stems with hydrocladia extending almost to base; stem internodes long with one or two pairs of opposite hydrothecae near middle of internode, node a constriction in perisarc. Hydrocladia up to 12 mm long, opposite, given off at an angle of 45° - 50° to stem from distal end of internode. Hydrocladial hydrothecae paired, distal on internode, not conjoined; internode somewhat constricted proximally, expanding to base of hydrothecae; hydrothecae of first one or two pairs on internode a little displaced relative to one another.

Hydrotheca tubular, expanding a little distally, perisarc smooth, adcauline wall almost straight proximally, gently convex distally, free part about one quarter total length of wall, base rounded with a small plug of perisarc; abcauline wall proximally tumescent, becoming concave to margin. Margin tilted upwards at an angle of 45° - 60° to hydrocladial axis, strongly sinuate, rim moderately everted, sometimes replicated several times. Hydranth small with about 10 tentacles.

Two kinds of nematocysts present:

- small ?mastigophores in tentacles, 9 µm long, discharged with difficulty,

- large isorhizas 45 - 50 x 12 - 13 µm, tubule up to 500 µm long and 1 µm diameter, armed throughout with spirals of short bristles; in hydranth and scattered throughout coenosarc; easily discharged.

Colonies dioecious, gonotheca arising on a long pedicel from deep within hydrotheca on stem and proximal parts of hydrocladia; male gonotheca long, straight to curved, elliptical, and flattened in frontal aspect; narrow in side view with up to eight deep, irregular corrugations fading proximally, corrugations shallower in frontal view, perisarc very thick; orifice circular, small, on a very short neck sealed by a plug of tissue. Female gonothecae on different stems from male, lenticular, shorter than male, with five or six irregular corrugations, orifice small, circular, on a short neck, sealed by a plug of tissue; gonophore one large or two small ova covered by a thick gelatinous pellicle, almost filling gonothecal cavity.

Colour. Living colonies reddish-purple.

Remarks. The above description is a composite from colonies collected by the author from several localities in Bass Strait, Victoria, Australia.

Apical stolonisation from stems and distally from the hydrocladia commonly occur in some colonies, the stolons often giving rise to new stems. While there is some variation in diameter of the hydrothecal rim and in length of the adcauline wall throughout the range of colonies examined, the free wall is always one quarter to one fifth of total wall length. There is no difference in size of hydrothecae between male and female stems. Large nematocysts are very abundant in most colonies.

Table 5. Measurements (µm) of specimens of *Syntheicum patulum* from Bass Strait, southern Australia.

	Eastern Bass Strait	Western Port	Port Phillip Bay	Range of dimensions
Hydrorhiza, diameter			300	300
Stem				
maximum diameter	280 - 340	240 - 300	260 - 300	240 - 340
length of internode	2,060 - 2,160	1,640 - 1,800	1,780 - 1,900	1,640 - 2,160
diameter at node	260	240 - 260	240 - 280	240 - 280
Hydrocladium				
internode length	608 - 672	552 - 560	600 - 672	552 - 672
diameter at node	152 - 168	144 - 152	152 - 168	144 - 168
Hydrotheca				
length of adnate adcauline wall	480 - 496	408 - 440	440 - 480	408 - 496
length of free adcauline wall	160	112 - 120	96 - 120	96 - 160
diagonal length abcauline wall	416 - 440	352 - 68	384 - 400	352 - 440
diameter at margin	192 - 216	144	128 - 184	128 - 216
Gonotheca				
width of male (lateral view)			360 - 460	360 - 460
width of male (frontal view)			560 - 600	560 - 600
length of female	960 - 1,100		1,100 - 1,300	960 - 1,300
width of female (lateral view)	480		360 - 400	360 - 480
width of female (frontal view)	520 - 620		460 - 560	460 - 620

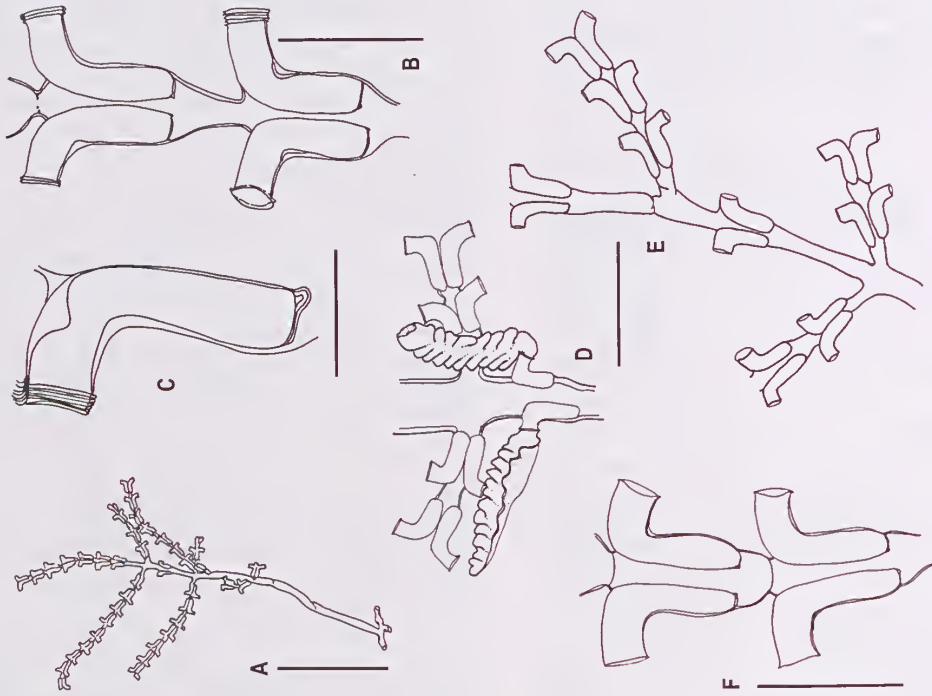


Fig. 32. *Syntheicum orthogonium*: A, stem from colony from Plater Rock. B, hydrocladial internode from same colony. C, hydrotheca with replicated and everted margin from same colony. D, gonothecae from same colony. E, stem fragment from Busk's holotype of *Syntheicum orthogonium*. F, hydrocladial internodes of Busk's holotype. Scale bars: A, 10 mm, B F, 500 µm; C, 200 µm; D, E, 1,000 µm.

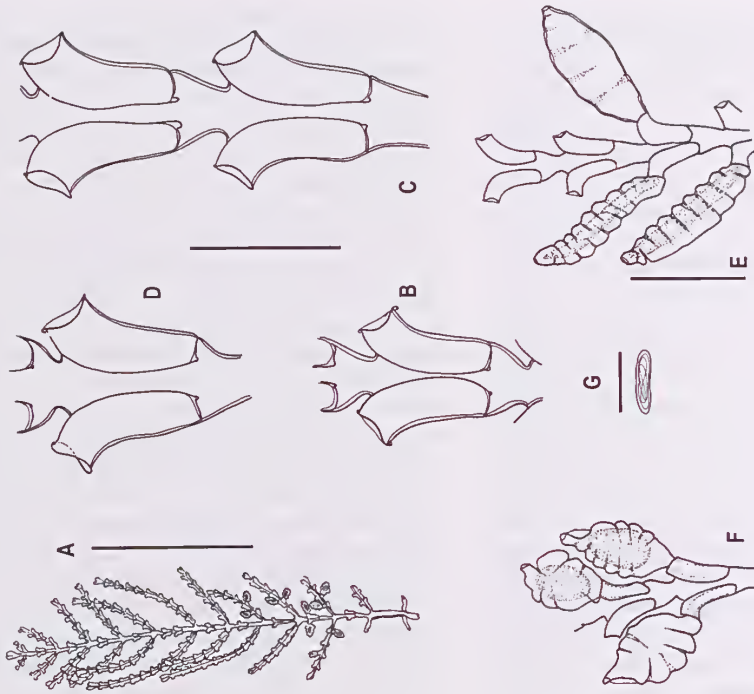


Fig. 33. *Syntheicum patulum*: A, fertile colony from Gabo Island, eastern Victoria. B, hydrocladial internode from same colony. C, hydrotheca from colony from Port Phillip Bay, Victoria. D, hydrocladial internode from colony from Backstairs Passage, South Australia. E, male gonotheca on colony from Western Port, Victoria. F, female gonotheca from colony from Port Phillip Bay. G, undischarged isorhiza from coenosarc of stem, colony from Western Port, Victoria. Scale bars: A, 10 mm; B - D, 500 µm; E, F, 1,000 µm; G, 50 µm.

Syntheceum patulum is a common hydroid of south-eastern ocean, coastal and deep water embayments. The distinctively purple-coloured colonies grow in tufts on rock, bryozoans, sponge and dead shell in good current flow. The species is fertile over the summer months.

Family Halopteridae Millard, 1962

Genus *Antennella* Allman, 1877

***Antennella secundaria* (Gmelin, 1791)**

(Fig 34A-D)

Sertularia secundaria Gmelin, 1791: 3856.

Aglaophenia secundaria - Lamouroux 1824: 19.

Antennella secundaria - Pennycuik 1959: 176.

- Watson 1973: 183. - Millard 1975: 332. - Ryland and Gibbons 1991: 525. - Ramil and Vervoort 1992: 143. - Medel and Vervoort 1995: 35. - Schuchert 1997: 14. - Calder 1997: 29 (full synonymy). - Watson 1996: 78. - Watson 1997: 522.

Antenella secundaria - Stechow and Müller 1923: 473.

Records and material. NTM C12993, microslide, colony from Stn 95. NTM C13046, alcohol preserved material; NTM C12991, microslide, colony from Stn 136. NTM C13047, alcohol preserved material, colony from Stn 84. NTM C12992, microslide, colony from Stn 111. Sparse, fertile colonies on alcyonarians, bryozoans and shellgrit. *Other records.* Stns 7, 37, 110, 82, 84, 95, 127.

Description. Hydrocladia up to 8 mm high, arising from a tubular hydrorhiza reptant on substrate; single nematothecae arising at intervals from hydrorhiza. Proximal part of hydrocladium with one to three athecate internodes, nodes transverse, each internode bearing one or two nematothecae, distalmost node strongly oblique. Hydrocladial internodes thereafter of similar length, alternately thecate and athecate, proximal node of thecate internode strongly oblique, passing beneath hydrotheca, distal node transverse below hydrothecal margin. Hydrotheca occupying almost entire internode, facing forward at an angle of c. 60° to hydrocladial axis, deep cup-shaped, walls almost parallel but abcauline wall sometimes faintly sinuate, free adcauline wall straight to slightly concave, adnate part convex, curving back to small hydropore at base of abcauline wall, perisarc thickened around base; margin circular, slightly sinuous.

Nematothecae bithalamic, small, two on athecate internode, basal chamber stout, cup small, foreshortened on adcauline side; mesial inferior stout, adcauline side of cup foreshortened, just reaching base of hydrotheca, lateral nematotheca borne on a long, slender pedicel where adcauline wall of hydrotheca becomes free, cup broad and shallow, excavated on adcauline side, not quite reaching hydrothecal margin; a small mesial superior nematotheca inserted beneath hydrotheca.

Gonothecae of both sexes borne on same hydrocladium, females in proximal region, males further along hydrocladium; female slipper-shaped, somewhat

flattened, facing forward, borne on a short, thick pedicel beside mesial inferior nematotheca; two large nematothecae at base of gonothecha; basal chamber of these long, cup wide, shallow, excavated on side facing gonothecha. Orifice of gonothecha distal, subcircular, closed by a thin operculum, gonothecha containing a single planula larva almost filling gonothecha at maturity. Male gonothecha considerably smaller than female, borne behind hydrotheca in same position as female, ovoid to kidney-shaped, flattened, apically blunt to rounded; no obvious orifice; a single small nematotheca at base, cup deeper and narrower than those on female; excavated on adcauline side. Spermatogenic mass almost filling gonothecal cavity.

Colour. Colourless, preserved material.

Measurements (µm).

Internode

length of athecate	
(along base of hydrocladium)	328 - 400
length of thecate	
(along base of hydrocladium)	168 - 272
diameter of transverse node	56 - 80

Hydrotheca

length of abcauline wall,	
margin to hydropore	176 - 224
diameter of margin	208 - 240

Nematothecae

mesial nematotheca, overall length	70 - 80
diameter of cup	24 - 32
lateral, overall length	74 - 92
diameter of cup	42 - 44

Gonothecha

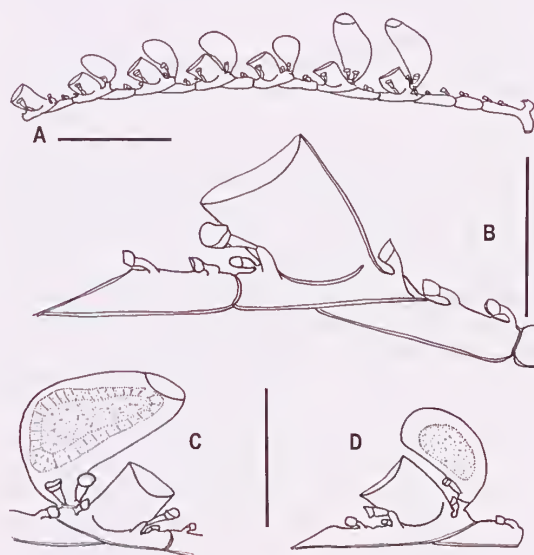


Fig. 34. *Antennella secundaria*: A, fertile hydrocladium. B, thecate and athecate internodes. C, female gonothecha. D, male gonothecha. Scale bars: A, 1,000 µm; B, 300 µm; C, D, 500 µm.

female, length of adcauline wall	544 - 632
maximum width	320 - 368
male, length of adcauline wall	280 - 344
maximum width	200 - 244

Remarks. The present material conforms with descriptions and dimensions of *Antennella secundaria* given by many authors (see Schuchert (1997)).

Distribution. Cosmopolitan in temperate and tropical seas.

Genus *Halopteris* Allman, 1877
***Halopteris polymorpha* (Billard, 1913)**
 (Fig. 35A-H)

Plumularia polymorpha Billard, 1913: 24.

Antennella polymorpha - Vervoort 1941: 218.

Plumularia buski Billard, 1913: 21. - Nutting 1927: 22. - Redier 1966: 90.

Halopteris buskii Rees and Thursfield, 1965: 160. - Vervoort and Vasseur 1977: 72. - Gibbons and Ryland 1991: 527. - Rees and Vervoort 1987: 119.

Halopteris polymorpha - Pennycuik 1959: 178. - Vervoort 1966: 132. - Millard and Bouillon 1973: 83. - Millard 1975: 354. - Millard 1978: 193. - Hirohito 1983, 62. - Ryland and Gibbons 1991: 530. - Schuchert 1997: 64.

Records and material. NTM C12937, alcohol preserved material; NTM C12995, microslide, colony from Stn 138. NTM C12998, microslide, colony from Stn 121. NTM C12994, microslide, colony from Stn 129. NTM C12996, microslide, colony from Stn 146. Colonies on shell grit. NTM C12938, alcohol preserved material; NTM C12997, MV F86902, microslides, colony on sponge from East Point reef, coll: J. E. Watson, depth 7 m, 17/81998.

Description. Hydorhiza short, tubular, ramified, of same diameter as stem. Stems to 20 mm high, monosiphonic, lower segments ahydrocladial, perisarc thick with irregularly spaced transverse nodes, distal lower stem with scattered nematothecae; first hydrothecate internode short with a strong proximal and V-shaped distal node, a hydrotheca just above node; cauline nodes thereafter oblique but less distinct, each with a hydrocladium and basal hydrotheca in lower third. Hydrocladial apophysis inserted alongside cauline hydrotheca, long, with transverse distal node, first hydrocladial internode athecate, short, with one proximal mesial nematotheca, distal node strongly oblique, internodes thereafter alternately hydrothecate and athecate, thecate internodes longer than athecate, two partial intranodal septa superior to hydrotheca. Hydrothecae variable in shape on different stems, from deep to shallow cup-shaped, seated in proximal to mid-region of internode at an angle of c. 45° to hydrocladial axis, free adcauline wall varying (on different stems) from almost straight to distinctly concave, base convex,

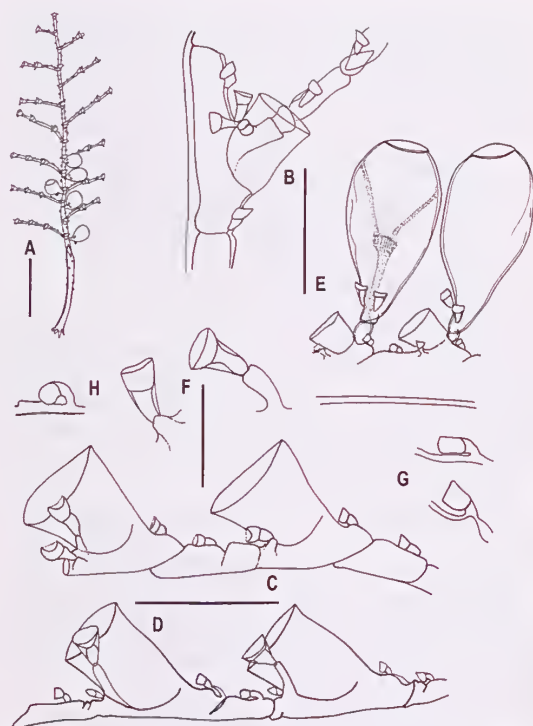


Fig. 35. *Halopteris polymorpha*: A, colony from Darwin Harbour. B, stem internode with hydrocladium. C, hydrocladial internode with cup-shaped hydrothecae. D, hydrocladial internode with cylindrical hydrothecae. E, female gonothecae. F, lateral nematothecae with short and long pedicels. G, mesial nematothecae. H, superior mesial nematotheca from below hydrotheca. Scale bars: A, 2,000 µm; B, E, 500 µm; F, G, H, 100 µm; C, D, 300 µm.

abcauline wall straight to slightly sinuous, expanding just behind margin. Margin circular, perpendicular to hydrothecal axis, perisarc rather thin.

Nematothecae all bithalamic; athecate internode with one mesial nematotheca on centre of internode with short, robust base, cup almost rectangular, adcauline side excavated, closely adpressed to hydrocladium; hydrothecate internode with one inferior mesial nematotheca similar to intersegmental nematotheca, not reaching base of hydrotheca; lateral nematothecae bithalamic, seated on pedicels of varying length, basal chamber moderately long, cup reaching to or just above hydrothecal margin, wide and shallow; adcauline side shallowly to deeply excavated; a small, superior mesial nematotheca inserted at base of hydrotheca. Cauline nematothecae same as mesial superior.

Female gonotheca large, balloon-shaped, widest distally, borne on a pedicel of one or two globular internodes beside cauline hydrotheca; two nematothecae similar to laterals side by side above pedicel; orifice terminal, elliptical to circular, closed by a slightly domed operculum.

Colour. Live colonies white.

Measurements (μm).

Stem			
diameter of athecate stem			120
length of first stem internode			424
length of succeeding internodes	360	-	400
diameter of nodes	56	-	64
Apophysis			
diameter at node	40	-	56
Hydrocladium			
length thecate internode	288	-	352
length of first intersegment	136	-	176
length of succeeding intersegments	88	-	120
diameter of transverse node	32	-	40
Hydrotheca (tubular form)			
length free adcauline wall	96	-	112
length abcauline wall	192	-	200
diameter of margin	160	-	168
Hydrotheca (cup-shaped form)			
length free adcauline wall	96	-	112
length abcauline wall	192	-	200
diameter of margin	160	-	168
Nematotheca			
length of pedicel of lateral	48	-	52
overall length of lateral	52	-	72
diameter of cup	44	-	52
Gonotheca			
length including pedicel	800	-	880
maximum width	376	-	440
diameter of operculum	192	-	224

Remarks. Both stems and hydrocladia show evidence of regeneration after breakage.

Colonies show two distinct hydrothecal morphologies (Fig. 35C, D) but all fall within the range of variation of *Halopteris polymorpha* defined by Schuchert (1997). The form with wider, cup-shaped hydrothecae resembles specimens from the Seychelles while those with more tubular hydrothecae are similar to those from Billard's (1913) Siboga Station 80 (see Schuchert 1997).

Relationship between *Halopteris buski*, *H. polymorpha* and *H. glutinosa* (Lamouroux, 1816). In a detailed study of the Halopterididae, Schuchert (1997) found that several species, including *Halopteris polymorpha*, have been confused with *Halopteris buski* (Bale, 1884). *Halopteris buski* from southern Australia can be confidently distinguished from *Halopteris polymorpha* only in fertile material, the female gonotheca of the former bearing up to 12 nematothecae in two rows compared with only two nematothecae at the base of the female of *H. polymorpha*. It is also clear from Kirchenpauer's figure of the female gonotheca of *Halopteris obconica* (Kirchenpauer, 1876) from southern Australia that *H. buski* is a synonym of that species.

Schuchert (1997) examined the remaining fragment of the type of *Halopteris glutinosa* (Lamouroux, 1816) from "mers des Indes et l'Australie" and suggested the possible conspecificity of *H. buski* with *H. glutinosa*. Although the condition of the type specimen was too

poor for accurate description, Schuchert's figure is typical of specimens from southern Australia referred by Bale (1884) to *H. buski*. Both Lamouroux (1816) and Bale (1884) commented on the distinctive scarlet colour of the species. Since only one species of hydroid from southern Australia has such distinctive colouration (J. E. W., pers. obsv.) it is certain that *H. obconica* and *H. buski* are conspecific with *H. glutinosa*.

Distribution. Indo-Pacific, Indian Ocean (Millard and Bouillon 1973) (Billard 1913), (Vervoort 1966), French Polynesia (Vervoort and Vasseur 1976). Tropical eastern Australia (Pennycuik 1959).

***Halopteris plagiocampa* (Pictet, 1893)**

(Fig. 36A-C)

Plumularia plagiocampa Pictet, 1893: 56. - Billard 1913: 31. - Jäderholm 1919: 21.

Halopteris plagiocampa - Schuchert 1997: 117.

Record and material. NTM C12998, microslide, infertile stem fragment in poor condition broken off from hydrorhiza, on *Idiellana pristin* from Stn 121.

Description. Stem 7 mm high, monosiphonic, perisarc very thin, smooth, internodes long with distinct transverse nodes, a row of four equidistant nematothecae on front of internode; opposite pairs of hydrocladia given off distally on internode. Hydrocladial apophysis short, with two transverse distal nodes; hydrocladia opposite, directed upwards at 35° - 60° to stem axis. Hydrocladial internodes variable in length, usually long and slender, proximal internode athecate with one small mesial nematotheca close to transverse proximal node, internodes thereafter with strongly oblique proximal node and transverse distal node. Hydrothecate internode shorter than proximal internode, hydrotheca seated on distal half. Hydrotheca deep, almost tubular, set at an angle of 40° to hydrocladial axis, floor shallowly convex, free adcauline wall short, decidedly concave, abcauline wall straight, margin circular, rim not everted.

Nematothecae all bithalamic, mesial proximal on athecate internode, small, basal chamber stout, cup shallow, broad, mesial inferior similar, basal chamber more robust, nematotheca not reaching base of hydrotheca; lateral nematotheca inserted without pedicel below adnate adcauline wall, not reaching hydrothecal margin, basal chamber long, cup shallow and broad, a little excavated on adcauline side; cauline nematothecae similar to mesials; no lateral nematothecae associated with cauline hydrotheca.

Colour. Transparent to colourless (preserved material).

Measurements (μm).

Stem			
length of internode	800	-	1,060
width at node	72	-	80
length of apophysis (abcauline side)	60	-	72
width of distal apophysal node	36	-	40

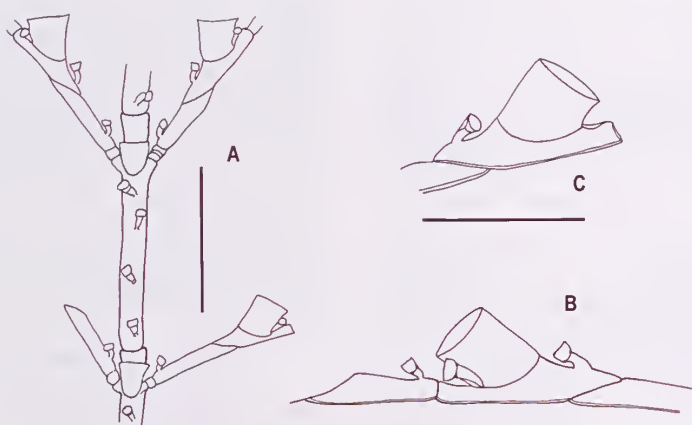


Fig. 36. *Halopteris plagiocampa*: A, part of stem. B, thecate hydrocladial internode. C, thecate hydrocladial internode with lateral nematothecae removed to show concave adcauline wall. Scale bars: A, 500 μ m; B, C, 300 μ m.

Hydrocladium	
length of athecate intersegment	208 - 312
length of thecate internode	184 - 272
diameter at transverse node	36 - 40
Hydrotheca	
length of abcauline wall	140 - 148
length of free adcauline wall	60 - 64
diameter at margin	124 - 140
Nematotheca	
length of pedicel	
of intersegment mesial	24 - 28
diameter of cup	24 - 36
length of pedicel of lateral	40 - 46
diameter of cup	38 - 42
length of mesial inferior pedicel	32 - 38
diameter of cup	30 - 32

Remarks. Schuchert (1997) distinguished *Halopteris plagiocampa* from its close congener *Halopteris zygocladia* (Bale 1914) on the shorter basal chamber and more inrolled cup of the lateral nematotheca of *H. zygocladia*. As the few reasonably well preserved nematothecae of the present material do not appear to have inrolled cups the specimen is here referred to *Halopteris plagiocampa*.

Distribution. Indonesia, Japan (Billard 1913, Jäderholm 1919). A new record for Australia.

Family Plumulariidae Hincks, 1868

Genus *Monotheca* Nutting, 1900

***Monotheca flexuosa* (Bale, 1894)**

(Fig. 37A, B)

Plumularia flexuosa Bale, 1894: 115. - Mulder and Trebilecock 1916: 79. - Stechow 1925: 246. - Blackburn, 1938: 315. - Shepherd and Watson 1973: 140. - Watson 1973: 188.

Monotheca flexuosa - Stechow 1921: 260. - Stechow 1925: 246.

Record and material. NTM C12999, microslide, small infertile colony on shell grit, from Stn 87.

Description. Stems to 5 mm high, flexuous, monosiphonic, unbranched, arising from a creeping tubular hydrotheca; perisarc of proximal stem fairly thick, nodes distinct, without nematothecae; internodes of hydrocladial stem region slender, expanding a little distally, nodes transverse, deeply incised, a nematotheca halfway along internode, one or two in axil of apophysis and one just below axil. Hydrocladia alternate, fairly short, proximal internode athecate, node narrow, slightly oblique, followed by hydrothecate internode; hydrotheca sunk into and projecting beyond end of hydrocladium, deeply campanulate, expanding to margin, abcauline wall weakly concave, adcauline wall almost straight, base rounded, margin circular, flaring but not everted.

Nematothecae all two-chambered, basal chamber of mesial inferior short, cup reaching base of hydrotheca, adcauline side foreshortened; twin laterals inserted in blunt apex of hydrocladium below hydrotheca, basal chamber long, cup circular, fairly wide and shallow; cauline and axillary nematothecae same as mesial.

Colour. Colourless.

Measurements (μ m).

Stem	
length of internode	200 - 304
diameter of node	20 - 24
length of apophysis	20 - 32
Hydrocladium	
length of athecate internode	68 - 80
length of hydrothecate internode	120 - 152
diameter of node	20 - 24
Hydrotheca	
length of abcauline wall	92 - 100
diameter of margin	100 - 120

Remarks. One to three axillary nematothecae are present in the specimens, thus differing from *Monotheca*

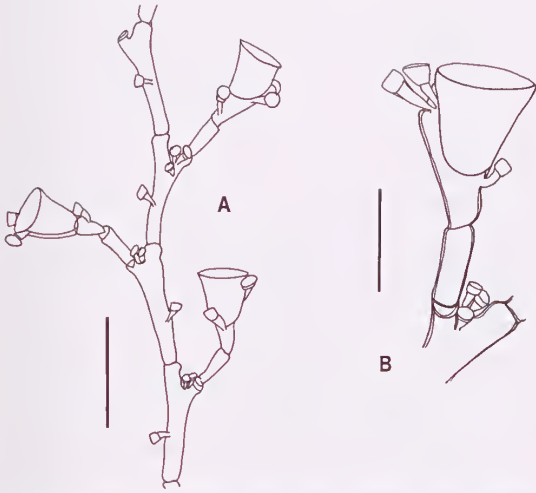


Fig. 37. *Monothecha flexuosa*: A, distal part of stem. B, hydrocladium. Scale bars: A, 1,000 µm; B, 100 µm.

flexuosa from southern Australia which usually has only one or two (J. E. W., pers. obsv.). While the significance of the third axillar nematotheca is not known in this tropical material, variation of the number of nematothecae is not regarded as a reliable diagnostic character.

In the absence of gonothecae, *Monothecha pulchella* (Bale, 1882) is virtually indistinguishable from *M. flexuosa*. The gonotheca of *M. pulchella* is large with a laterally directed terminal orifice and large internal submarginal teeth while that of *M. flexuosa* is more elongate with an axially directed terminal orifice and sometimes a raised collar. This difference may possibly be sexual as all gonophores of *M. flexuosa* so far found in southern Australia are female (J. E. W., pers. obsv.); the gonophore of *M. pulchella* is still unknown.

Distribution. Southern Australia and South Africa. Not previously recorded from tropical Australia.

Genus *Nemertesia* Lamouroux, 1812

Nemertesia cylindrica (Kirchenpauer, 1876)

(Fig. 38A-E)

Plumularia cylindrica Kirchenpauer, 1876: 45.

Antennularia cylindrica - Bale 1884: 146.

?*Nemertesia cylindrica* - Nutting 1927: 227.

- Pennycook 1959: 178.

Records and material. NTM C12961, alcohol preserved material; NTM C13000, NTM C13002, MV F86906, microslides, colony from Stn 146. NTM C13001, microslide, colony from Stn 121. NTM C12962, alcohol preserved material; NTM C13013, microslide, colony from Stn 136. MV F86948, alcohol preserved material, colony from Stn 147. Fertile and infertile small to medium size colonies attached to rock. **Other records,** Stns 91, 137, 139. East Arm breakwater and channel bed,

many large colonies, coll: J. E. Watson depth 6 m, 20/8/98. Plater Rock channel bed, many large colonies on rock, coll: J. E. Watson, depth 15 m, 22/9/1999.

Description. Colonies to 200 mm high, up to 30 stems arising from a large fibrous, hydrorhizal mat up to 50 mm wide; stolons also enmeshing basal region of stems in a spongy sheath. Stems erect, long, monosiphonic, single or forked at an acute angle more or less in the same plane, internodes thick, short, nodes transverse, deeply incised in proximal and distal stem regions, often indistinct in mid-stem region.

Hydrocladia crowded, arising at an acute angle in verticels of up to eight around each internode, reducing to four or five in distal stem region. Apophyses with a short, slightly oblique, often indistinct node, a truncated tubular mamelon on adcauline side. Hydrocladial internodes long, straight, nodes distinct, slightly oblique, sometimes replicated. Hydrotheca occupying more than half of internode, tubiform, adcauline wall completely adnate, weakly convex, posterior wall slightly convex to straight, abcauline wall slightly sinuous, margin circular, cut obliquely away to join internode.

Mesial inferior nematotheca seated on a prominence of the internode, lying along internode to touch base of hydrotheca, bithalamic, basal chamber long, tapering, freely movable, cup deep, excavated on adcauline side; lateral nematotheca bithalamic, seated on a minute pedicel at hydrothecal margin, basal chamber short, inflated, side of cup deeply excavated and closely adpressed on side facing hydrotheca, obscuring hydrothecal margin. Cauline nematothecae same as mesials, one on each side of stem internode, just proximal to node, two or three flanking mamelon at base of apophysis.

Female gonothecae large, distributed along entire length of stem, several on internode, upwardly tilted, without pedicel, irregularly saccate to sausage-shaped (depending on angle of view), perisarc moderately thick, up to eight nematothecae similar to laterals distributed along frontal margin, orifice distal, subcircular to elongate, flanked by two blunt lateral lobes, orifice closed by a sheet of tissue, gonotheca containing three globular planulae.

Colour. Stems of live colonies dark shining brown, hydrocladia and gonothecae paler brown to almost white.

Measurements (µm).

Stem	
length of internode	460 - 500
width at node	400 - 600
Hydrocladium	
maximum length	5,000
length of internode	448 - 464
width at node	80 - 96
Hydrotheca	
length of abcauline wall	224 - 256

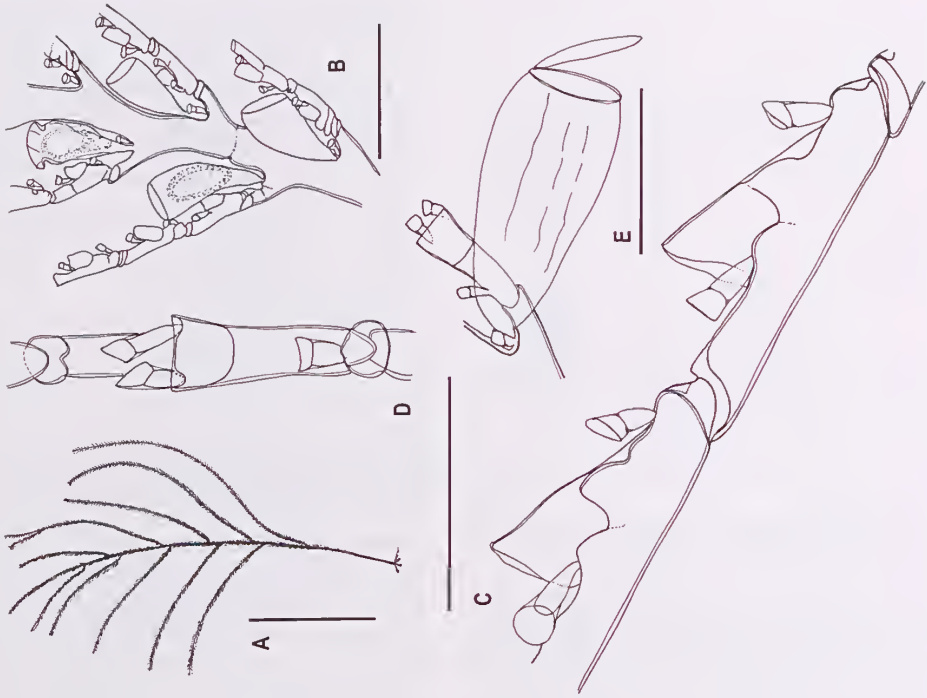


Fig. 39. *Plumularia badia*: A, one stem from tall colony from East Point reefs. B, part of fertile stem from Beagle Gulf. C, hydrocladium. D, hydrotheca, anterior view. E, gonothecha. Scale bars: A, 50 mm; B, 500 µm; C, D, 200 µm; E, 300 µm.

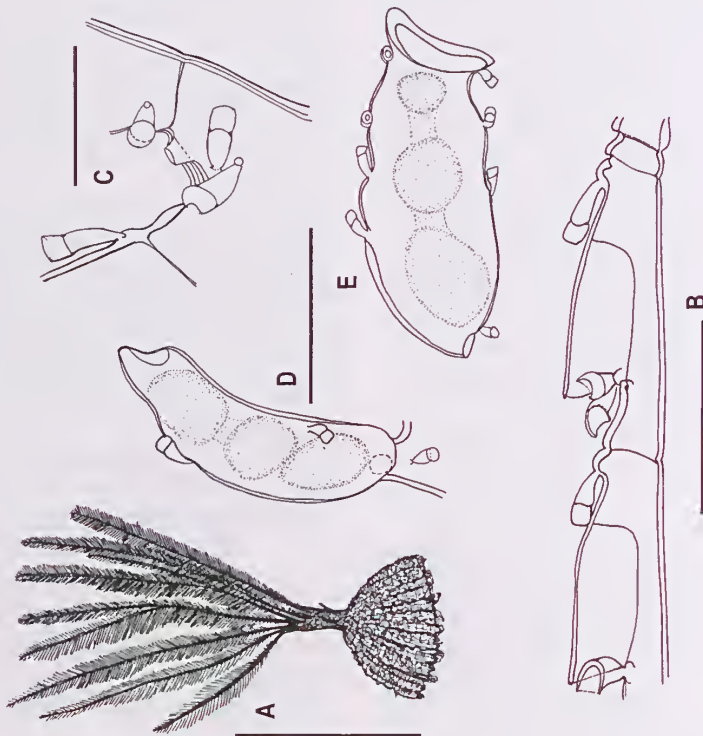


Fig. 38. *Nemertesia cylindrica*: A, colony from East Arm breakwater. B, hydrocladium from same colony. C, apophysis of stem with cauline nematothecae and axillary mamelon. D, lateral view of female gonothecha. E, frontal view of female gonothecha. Scale bars: A, 50 mm; B, 300 µm; C, 200 µm; D, E, 500 µm.

width at margin	80 - 96
Nematotheca	
overall length of median	92 - 100
depth of cup	32 - 48
overall length of lateral	72 - 80
Gonotheca	
length	800 - 1,040
width (frontal view)	340 - 400
width (lateral view)	176 - 240

Remarks. The abundant fertile material in the Beagle Gulf and Darwin Harbour collection led to re-appraisal of *Nemertesia cylindrica* (Kirchenpauer, 1876) and *N. indivisa* (Allman, 1883). *Nemertesia cylindrica* was erected on infertile material from Java, and Allman described *N. indivisa* from fertile specimens with lobate gonothecae from Cape York, Australia. Billard (1913) referred specimens from Indonesia with lobate gonothecae to *N. indivisa* and included *Antennularia cylindrica* Bale, 1884 from off Port Curtis, Queensland, in its synonymy. After examination of type material of *N. indivisa*, Bale (1919), following Billard (1913), wrongly concluded that *N. indivisa* and *N. cylindrica* were conspecific. Nutting (1927) and Pennycuik (1959) recorded, without adequate description or figures, *N. cylindrica* from the Philippines and Queensland respectively; because of lack of description, their records are doubtful. Billard (1913) described *N. indivisa* as having two pairs of axillary nematothecae and his figure depicts a complex lobate gonotheca. The Beagle Gulf material usually has two, sometimes three but never four axillary nematothecae. This, together with the completely different gonotheca shows that the material cannot be *N. indivisa*. As comparative measurements of the Beagle Gulf material agree with those extracted from Bale's (1884) figure of *Antennularia cylindrica* (pl. 10, fig. 7) it is concluded that the two are conspecific. This is the first record of the gonosome of *N. cylindrica*. Being very difficult to distinguish when infertile, it is unfortunate but understandable that *A. cylindrica* and *Nemertesia indivisa* were confused by earlier authors; they are, however, easily separated when fertile.

Colonies of *Nemertesia cylindrica* observed in Darwin Harbour are distinctive in their large size, the dark brown brush-like bunch of tall, straight stems emerging from a large, spongy hydrorhizal mass which sheaths and binds the lower stems firmly together, at the same time anchoring it in situations of strong current flow (J. E. W., pers. obsv.).

Distribution. Australian tropical east coast (Pennycuik, 1959).

Genus *Plumularia* Lamarck, 1816
***Plumularia badia* Kirchenpauer, 1876**
 (Fig. 39A-E)

Plumularia badia Kirchenpauer, 1876: 45. - Bale 1884: 128. - Bale 1913: 135. - Thornely 1916: 149. - Jäderholm

1916: 7. - Stechow and Müller 1923: 473. - Vervoort 1941: 221. - Watson 1996: 79.

Plumularia ramsayi Bale, 1884: 131. - Kirkpatrick 1890: 604. - Billard 1913: 52.

Plumularia gracilis von Lendenfeld, 1885b: 476.

Records and material. NTM C13003, NTM C13004, NTM C13005, NTM C13006, MV F86905, microslides, colony from Stn 52. NTM C13007, microslide, colony from Stn 95. NTM C12900, MV F86940, alcohol preserved material, East Arm channel and breakwater, coll: J. E. Watson, depth 7 m, 19/8/1998. NTM C12901, alcohol preserved material, East Point reef, immature and richly fertile mature colonies on dead coral boulders, coll J. E. Watson, depth 6 m, 19/9/1999. *Other records.* Stns 58, 67, 101. Plater Rock, many large fertile colonies on sponges, coll: J. E. Watson, depth 8 m, 21/9/1999.

Description. Hydrorhiza a tangle of narrow tubes entwining substrate. Colonies ranging from single, branched stems 20 mm high to large clusters of 60 complexly branched stems 240 mm high. Stems slender, monosiphonic, more or less alternately branched in same plane, lower stem region ahydrocladial, hydrocaulus of short stems stiff, branching pseudosympodial, almost perpendicular to cauline axis; stems of taller colonies long, flexuous, subdichotomous branching common to second or third order, branches directed acutely upwards, distally truncated. Stem and branch internodes short, smooth, nodes transverse, deeply incised proximally, fading distally, a node below and above origin of each branch, branch apophysis with oblique distal node. Perisarc of stem and branches smooth and thick.

Hydrocladia alternate, short, two on branch internode, in distal region of branch one row sometimes slightly displaced to front of branch with a third above, forming a verticil; hydrocladia backwardly curved, inserted on a long, geniculate, upwardly directed apophysis with a strong oblique distal node; two nematothecae in axil and a mamelon with short neck on apophysis distal to nematothecae. Hydrocladial internodes all hydrothecate, variable in length, node deeply oblique, a weak septum projecting downwards into internode from adcauline wall of hydrotheca. Hydrotheca deep cup-shaped, centrally placed on shorter internodes, proximal on longer internodes, adcauline wall immersed in internode, posterior wall perpendicular to internode, curved, abcauline at an angle of 30° to internode, wall straight, or with a slight concavity behind margin; margin sinuate, base excavated back into internode.

Nematothecae bithalamic, large, moveable, mesial inferior borne on a low prominence of internode, a deep perisarc-infilled notch in front, basal chamber of nematotheca long, cup foreshortened on adcauline side, not reaching base of hydrotheca; twin laterals similar to mesial, inserted on a prominence behind hydrothecal margin, projecting forward from margin, facing inwards towards axis of internode, cup shallowly excavated on

adcauline side. Cauline nematothecae same as laterals, one beside apophysis (often absent) and one in axil, a small mamelon or pore on base of apophysis between nematothecae.

Gonotheca inserted without pedicel in axil of branch apophysis, small, conical, distally truncated, terminal orifice circular, sealed by a thin opercular flap, perisarc very thin.

Colour. Stem and branches of live and preserved specimens shining dark brown to black, hydrocladia whitish, gonothecae transparent white.

Remarks. Variations in dimensions of hydrothecae occur throughout the colonies, some having a longer abcauline wall and a narrower margin than usual. The thickened, truncated apex of the branches noted by Kirchenpauer (1876) which suggests breakage occurs so consistently that it must be a normal habit of growth. While hydrocladia are alternate on older parts of the stems, the distal regions of some branches have hydrocladia in verticils of three, approaching the structure of *Nemertesia*. The gonothecae are so delicate that most collapse in mountant. There is some evidence that the gonophore may be expelled as an acrocyst.

The large amount of material examined in the present study and the wide range in some critical morphological dimensions supports comments on the variability of *Plumularia badia* by previous authors. But for the finding of some colonies of intermediate size, the short-stemmed, pseudosympodially branched form of *P. badia* could easily be mistaken for a different species from the tall form (Table 6). Such structural differences may be a response to ecological conditions, the simply branched, shorter, presumably juvenile morphology being lost as colonies increase in height and in number of stems. The

long tresses of the tall form occur on sponges and other invertebrate substrates in strong current flow of tidal channels, whereas the shorter, pinnate colonies occupy more sheltered habitats on reefs.

Plumularia badia is one of the most abundant species in Darwin Harbour.

Distribution. Indonesia and Torres Strait, Australian subtropical and tropical coasts (Bale 1884, Watson 1996).

Plumularia scabra Lamarck, 1816 (Fig. 40A-E)

Plumularia scabra Lamarck, 1816: 127. - Billard 1907: 322. - Billard 1913: 47. - Bale 1919: 342. - Rees and Thursfield 1965: 164.

Plumularia effusa Busk, 1852: 388, 400. - Kirchenpauer 1876: 46. - Bale 1884: 129. - Bale 1887: 22.

Acanthella effusa - Allman, 1883: 27. - Marktanner-Turneretscher, 1890: 260. - Kirkpatrick, 1890: 610. - von Campenhausen, 1897: 315. - Stechow and Müller, 1923: 474.

Records and material. NTM C12897, alcohol preserved material; NTM C13008, MV F86903, microslides, colony from Stn 147. NTM C12896, MV F86930, alcohol preserved material, Stn 137. NTM C13014, microslide, Stn 136. Infertile colonies of few to many stems. NTM C12898, alcohol preserved material, Plater Rock, large colonies on rock, coll: J. E. Watson, depth 15 m, 22/9/1999. *Other record*, Stn 80.

Description. Hydrothiza a knot of thin, tough tubes. Colony consisting of up to 15 monosiphonic stems to 300 mm high, greater length of stems unbranched, distal stem region a branched canopy with up to three orders of branching into verticils, a deep hinge joint above fork on each branch. Branch internodes variable in length, becoming shorter distally, nodes collar-shaped, deep, internodes of younger branches bearing four hydrocladia, older branches bearing up to 10; apices of some branches with two or three thick, upwardly directed apophysal spines without hydrocladia. Perisarc of stems and branches very thick, thinning a little distally.

Hydrocladial apophyses very long, upwardly directed with a strongly oblique distal node and deep creases in perisarc; hydrocladia alternate, short, on front of branch, close-set on younger branches, directed forward and slightly reflexed, older branches with whorls of up to six hydrocladia. Hydrocladial internodes short, nodes strongly oblique, narrow, one to four intranodal septa, one passing into hydrocladium midway along adcauline wall of hydrotheca, another at base of lateral nematotheca, one, hook-shaped, below posterior margin of hydrotheca and one, not always present, behind node. Hydrotheca small, occupying almost entire internode, tubiform, abcauline wall sinuous, curving upward to margin, adcauline wall convex, immersed in hydrocladium, margin broadly lobate, excavated back to internode.

Table 6. Comparative measurements (μm) of short (simple) and tall (multiple) forms of *Plumularia badia*.

	Tall form		Short form	
Stem, width at base	1,000		800	
Branch				
length of distal branch	272	- 520	560	- 936
internode				
width at node	176	- 224	160	- 176
length of apophysis	120	- 136	72	- 104
(adcauline side)				
Hydrocladium				
maximum length	1,500	- 1,720	1,400	- 1,700
length of internode	236	- 280	296	- 352
width at node	36	- 60	36	- 40
Hydrotheca				
length of abcauline wall	80	- 100	80	- 96
width of margin (lateral view)	56	- 88	64	- 72
Nematotheca				
mesial, length of pedicel	30	- 32	32	- 40
width of cup		30	24	- 26
lateral length of pedicel	40	- 50	32	- 40
width of cup	30	- 38	26	- 34
Gonotheca				
length	256	- 336	480	- 560
distal width	136	- 160	200	- 240

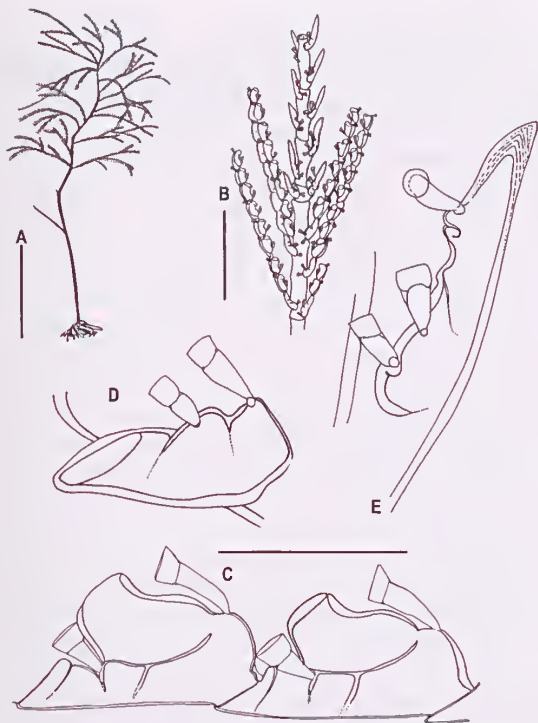


Fig. 40. *Plumularia scabra*: A, stem from colony from Beagle Gulf. B, hydrocladate part of stem with cauline spurs. C, hydrocladial internodes. D, apophysis of branch. E, cauline spur. Scale bars: A, 50 mm, B, 1,000 µm; C, D, E, 200 µm.

Nematothecae large, all of similar shape, bithalamic, movable, basal chamber long, one mesial inferior on prominence of internode at base of hydrotheca, cup deep, adcauline side slightly foreshortened, adpressed into curve of abcauline hydrothecal wall or standing erect; lateral nematotheca inserted without pedicel below hydrothecal margin, basal chamber shorter than that of mesial, cup level with hydrothecal margin; two or three cauline nematothecae associated with apophysis - one axillar, facing inwards to branch, another about halfway along apophysis, the third (if present) at base of distal apophysal node.

Colour. Stem and branches of live colonies grey-brown, fading to lighter brown, hydrocladia grey-white.

Measurements (µm).

Branch	
length, younger branch internode	760 - 800
width at node	96 - 136
Apophysis	
length abcauline wall	216 - 240
Hydrocladium	
length internode	200 - 216
width at node	40 - 52
Hydrotheca	
length abcauline wall	88 - 100

width at margin	76 - 100
Nematotheca	
length basal of chamber of mesial	48 - 64
marginal width of mesial cup	42
depth of cup (abcauline wall)	20 - 24
length of basal chamber of lateral	26 - 30
marginal width of lateral cup	24 - 26
depth of cup (abcauline wall)	26

Remarks. Although Lamarck's brief description of *Plumularia scabra* was accurate, Bale (1884) doubted the validity of the species but Billard (1907) in redescription of the type in the Lamarck collection of the Muséum du Paris confirmed the accuracy of Lamarck's description. Dimensions of the present material fall within the range of variation of the type. The apical apophysal spurs are diagnostic of the species.

Seen *in situ*, the colonies are tall with up to 15 stems and a sparse, gracefully branching canopy. The species prefers open, rocky habitat in good current flow at depths greater than 15 m at the base of reefs.

Distribution. "South Seas" (Lamarck 1816), Philippines, Indonesia (Billard 1913), Torres Strait (Busk 1852).

Plumularia setacea (Linnaeus, 1758)
(Fig. 41A, B)

Sertularia setacea Linnaeus, 1758: 813.

Plumularia setacea - Lamarck 1816: 129. - Hincks 1868: 296. - Bale 1888: 778. - Billard 1913: 32. - Ritchie 1911: 851. - Bale 1915: 294. - Pennycuik 1959: 180. - Ralph 1961: 33. - Millard 1975: 399. - Watson 1994: 67. - Cornelius 1995: 158. - Watson 1996: 79.

Plumularia tripartita von Lendenfeld, 1885b: 477.

Record and material. NTM C13009, microslide, damaged infertile stem on *Eunice tubifex*, Stn 40. *Other record.* Fragmentary stem, Stn 137.

Description. Stems to 4 mm high, cauline internodes long, slender, widening distally to a distinct, transverse node; internode bearing one to three nematothecae, if all three present, equally spaced along internode, distalmost just below hydrocladial apophysis; if only one, this usually proximal on internode. Perisarc of stem thick proximally, thinning distally and along hydrocladia. Hydrocladia alternate, inserted on an upwardly tilted distal apophysis; apophysis with one or two strong transverse nodes followed by a slightly oblique distal node; first hydrocladial internode hydrothecate, internodes thereafter alternately athecate and thecate; two or three hydrothecate internodes on hydrocladium, internodes long and slender, nodes slightly oblique, distinct; thecate internode widening from proximal node to base of hydrotheca

Hydrotheca on distal third of internode, abcauline wall confluent with internode, adcauline wall almost entirely adnate, convexly curved, free part short, straight, margin circular, tilted distally at an angle of c. 105° to

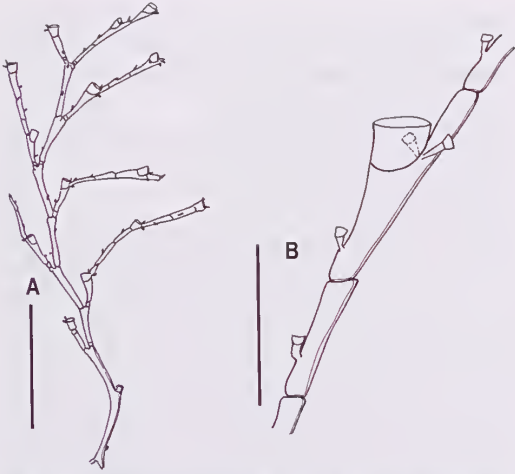


Fig. 41. *Plumularia setacea*: A, stem from Beagle Gulf. B, hydrocladial internodes. Scale bars: A, 1,000 µm; B, 300 µm.

hydrocladial axis; athecate internode with a small mesial nematotheca at proximal third to centrally placed, inclined towards hydrocladium, basal chamber short, robust, cup a little foreshortened on adcauline side; mesial nematotheca proximal on hydrothecate internode, same as athecate mesial; lateral nematotheca small, freely movable, facing outwards, basal chamber inserted without pedicel in internode beneath hydrotheca, cup small, circular; cauline nematothecae same as mesials. Perisarc of hydrocladia and hydrotheca thin; hydranth with 12 - 14 tentacles.

Colour. Colourless, preserved material.

Measurements (µm).

Stem	
length of internode	416 - 504
diameter at node	40 - 48
Hydrocladium	
length of athecate internode	200 - 240
length hydrothecate internode	336 - 400
diameter at node	32 - 40
Hydrotheca	
length of abcauline wall	68 - 80
diameter of margin	100 - 104

Remarks. The specimen agrees with dimensions of *Plumularia setacea* given by Ritchie (1911) for specimens from the Australian east coast.

Distribution. Cosmopolitan. Recorded from east, west and southern Australia.

***Plumularia bedoti* (Billard, 1911)**
(Fig 42A-D)

Plumularia bedoti Billard, 1911: 64. - Billard 1913: 27.

Record and material. NTM C13010, microslide, two small, damaged infertile stems on *Gymnangium longicorne*, Stn 136.

Description. Stems to 10 mm high, proximal half of stems and lower branch lightly fascicled, becoming monosiphonic in upper region, apophysis of branch with transverse distal node, branch ahydrocladate proximally, internodes thereafter with strongly oblique nodes, each internode with three alternate, equidistant hydrocladia, one proximal, one in middle and one distal on internode. Perisarc of stem and branches thick and smooth. Hydrocladia frontal on stem and branches, internodes slender, first internode athecate, distal node oblique, internode with one mesial nematotheca, internodes thereafter alternately thecate and athecate; thecate internode with oblique proximal and transverse distal node, transverse node sometimes indistinct; no intranodal septa. Hydrothecae seated on upper side of internode, tubular, deep, occupying almost entire internode, tilted forward at an angle of c. 55° to internode, adnate adcauline wall convex, short, free adcauline wall straight, abcauline wall weakly convex, margin perpendicular to hydrothecal axis, subcircular to oval, rim slightly everted.

Nematothecae bithalamic, mesial hydrothecate inferior seated on a small prominence, a perisarc infilled notch between basal chamber and proximal node, basal chamber short, robust, cup foreshortened on adcauline side, just reaching base of hydrotheca; basal chamber of lateral nematotheca long, conical, movable, cup broad and shallow, reaching hydrothecal margin, excavated on adcauline side. Athecate internode with one mesial nematotheca similar to mesial inferior, proximal on internode, bent forward. Cauline nematothecae similar to mesials, a row of five on internode, one near base of apophysis, one above and one in axil.

Colour. Colourless to white, preserved material.

Measurements (µm).

Stem, maximum width	160
Branch	
diameter monosiphonic region	72 - 88
length apophysis abcauline wall	56 - 64
distance between hydrocladia on same side	344 - 376
Hydrocladium	
length along base intersegment	120 - 144
length along base hydrothecate internode	88 - 100
width at transverse node	20 - 36
Hydrotheca	
length free adcauline wall	60 - 76
length abcauline wall	104 - 128
diameter of margin	80 - 84
Nematotheca	
mesial, length of basal chamber	18 - 24
mesial, diameter of cup	18 - 20
lateral, length basal chamber (excluding pedicel)	28 - 34
lateral, diameter of cup	30 - 32

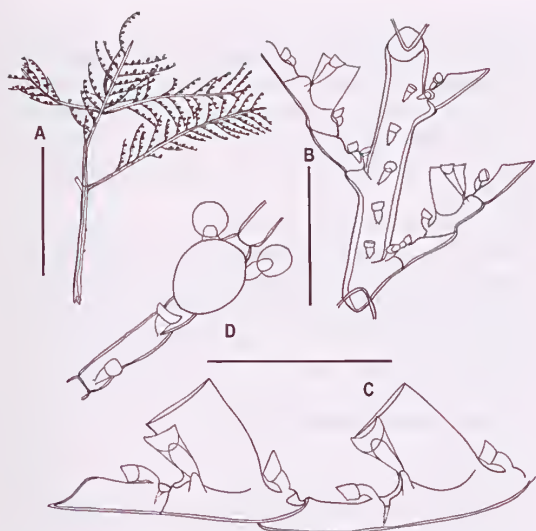


Fig. 42. *Plumularia bedoti*: A, stem from colony on *Gymnangium longicorne*. B, hydrocladate part of stem. C, hydrocladial internodes. D, anterior view of hydrotheca. Scale bars: A, 3,000 µm; B, 300 µm; C, D, 200 µm.

Remarks. Although the colonies are much smaller than those of *Plumularia bedoti* described by Billard (1913), they conform in morphological characters and dimensions with that species. The apophysial mamelon mentioned by Billard is not evident in the Beagle Gulf specimens.

Distribution. Previously known only from Indonesia (Billard 1913).

Plumularia tubacarpa sp. nov.

(Fig. 43A-D)

Material and record. Holotype, NTM C13011, microslide, infertile stem on sponge amongst shellgrit, Stn 87. (No preserved material).

Description. Hydorrhiza a small knot of tubular stolons. Stem 9 mm high, monosiphonic, slender, erect, internodes long, smooth, increasing slightly in diameter distally, nodes transverse, caulus slightly tumescent above node, nodes becoming fainter distally along stem. Hydrocladia alternate, one to four, usually two on internode, given off from a long, slender upwardly directed apophysis on side of stem; apophysis with an oblique distal node and frequently a transverse septum behind node; hydrocladia directed upwards at an angle of c. 35° to internode, with up to 10 hydrothecae. Hydrocladial internodes all thecate, nodes strongly oblique, an incipient septum passing into internode between base of hydrotheca and mesial nematotheca.

Hydrotheca seated in middle of internode, deep cup-shaped, adcauline wall entirely adnate, convex, abcauline wall contiguous at an angle of 20° with internode, straight to faintly sinuous, concave just behind margin; margin

circular, rim slightly everted and inclined slightly to hydrocladial axis. Nematothecae all same shape and size, bithalamic, moveable, basal chamber long, cup foreshortened on adcauline side; mesial inferior seated on a prominence of internode, standing erect, not reaching base of hydrotheca; lateral nematotheca inserted on a minute pedicel behind hydrothecal margin, extending well beyond hydrotheca. Cauline internodes with variable number of nematothecae, one in axil of apophysis, one beside apophysis, one halfway between hydrocladia and sometimes one at side of internode just above node.

Gonotheca long, tubular, pointing downward, inserted without pedicel on proximal side of apophysis in lower stem region, distal end domed, perisarc smooth.

Colour. Colourless.

Measurements (µm).

Stem	
proximal diameter	88
distal diameter	168
distance between hydrocladia	
on same side	640 - 768
apophysis, adcauline length	76 - 88
Hydrocladium	
length of internode	376 - 416
width at node	24 - 32
Hydrotheca	
length of abcauline wall	112 - 136
width at margin	96 - 112
Nematotheca	
median, overall length	52 - 60
diameter of cup	24
Gonotheca	
length	840
width	88

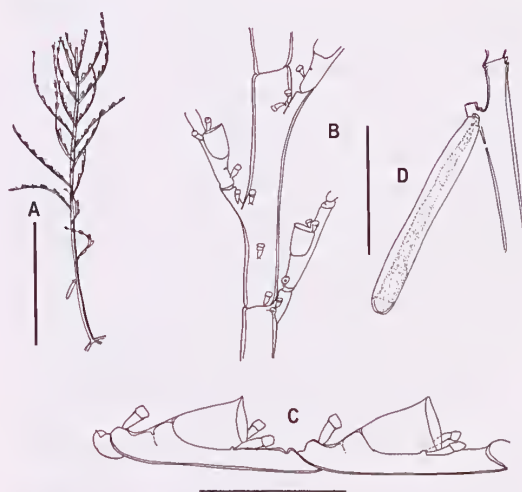


Fig. 43. *Plumularia tubacarpa* sp. nov. A, holotype colony. B, hydrocladate part of stem. C, hydrocladial internodes. D, gonotheca. Scale bars: A, 2,000 µm; B, D, 500 µm; C 300 µm.

Remarks. The single stem of *Plumularia tubacarpa* appears to be young, the distal cauline internodes still being poorly developed and there is a distinct growing apical tip. The long, tubiform gonotheca containing coenosarcal tissue also appears to be immature.

Plumularia tubacarpa does not resemble any species of *Plumularia* in available literature. While some species reported from Indonesia have spatulate to rectangular gonothecae (e.g. *P. insignis* var. *gracilis* Billard, 1913 and *P. spiralis* var. *longithecata* Billard, 1913) the absence of intranodal septa in the hydrocladium distinguishes *P. tubacarpa* from *P. insignis* and the presence of two, not three axillar nematothecae distinguishes it from *P. spiralis*. The hydrorhiza of *P. tubacarpa* is intergrown with that of a young colony of *Polyplumaria cornuta* for which species it was originally mistaken.

Etymology. Refers to the long, tubular gonotheca.

Genus *Polyplumaria* G. O. Sars, 1874

***Polyplumaria cornuta* (Bale, 1884)**

(Fig. 44A-F)

Plumularia cornuta Bale, 1884: 132.

Polyplumaria cornuta - Billard 1913: 53. - Briggs and Gardner 1931: 191.

Record and material. NTM C12940 alcohol preserved material, colony from Stn 67. NTM C12939, alcohol preserved material; NTM C13012, MV F86904, microslides, colony from Stn 92. Sparse fertile colonies on shellgrit and gravel. *Other records.* Stns 66, 87. East Arm channel, infertile colony on coarse sand, coll: J. E. Watson, depth 6 m, 21/8/1998.

Description. Hydrorhiza a tangle of thin colourless stolons embedded in shellgrit. Stems solitary, to 280 mm long, slender and flexuous, a proximal region short to long and sometimes lightly fasciated, stem thereafter hydrocladate, monosiphonic; distal half to third of stem branched in verticels of three, branches short, reflexed, hydrocladate. Perisarc of stem and branches thick, smooth. Hydrocladia on branches alternate, on an indistinct apophysis, hydrocladial internodes thecate, short, nodes strongly oblique, deep, three strong septa passing downwards from base of hydrotheca almost through internode; two partial septa, one below mesial nematotheca and between lateral nematotheca and node. Apophyses of some branches with a spinous accessory hydrocladium with several intrathecal septa, one or two nematothecae near apex and one hydrotheca with twin laterals but no mesial nematotheca. Hydrotheca adnate to internode, adcauline wall obscured by three humps associated with intranodal septa, abcauline wall weakly sinuous with a small peak behind margin; margin strongly sinuate, cut back to meet internode.

Nematothecae all bithalamic, movable, mesial inferior on a small prominence of internode, an infilling of perisarc at base, nematotheca standing almost erect, basal

chamber long, slender, cup shallow, foreshortened on adcauline side to almost triangular; basal chamber of lateral moderately long, inserted at base of hydrothecal margin, cup rather shallow, broad, a little excavated on adcauline side. Cauline nematothecae similar to mesial; three on internode, one at base of apophysis and two in axil.

Gonotheca inserted without pedicel in axil of apophysis, small, almost triangular, widening distally, no operculum, perisarc very thin.

Colour. In life, very pale yellow-brown, lower stems darker brown.

Measurements (μm).

Branch		
distance between hydrocladia		
on same side	580	- 800
Hydrocladium		
maximum length of hydrocladium	4,400	-6,000
length of internode	296	- 320
width at node	60	- 72
length of apophysial spine	260	- 280
Hydrotheca		
length of abcauline wall	176	- 180
width of margin	140	- 148

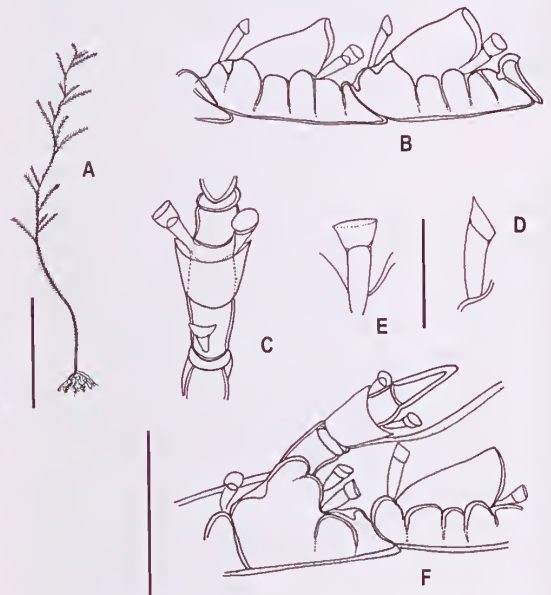


Fig. 44. *Polyplumaria cornuta*: A, colony from East Arm channel, Darwin Harbour. B, hydrocladial internodes. C, anterior view of hydrocladium. D, mesial nematotheca. E, lateral nematotheca. F, cauline spur. Scale bars: A, 50 mm; B, C, 300 μm ; D, E, 100 μm ; F, 300 μm .

Nematothecae

mesial inferior, length of basal chamber	66 - 90
diameter of cup	30 - 40
lateral, length of basal chamber	64 - 76
diameter of cup	44 - 52

Gonotheca

length	66 - 100
distal width	40 - 54

Remarks. The graceful, slender colonies tend to collapse out of fluid. The few gonothecae present on one colony are too poorly preserved and obscured by adventitious matter for determination of sex. Except for the absence of the mesial nematotheca associated with the hydrotheca on the accessory hydrocladium the present material conforms with the detailed description and dimensions of *Polyplunaria cornuta* given by Billard (1913).

Colonies occur in sandy beds of channels in strong current flow, their pale colour rendering them almost invisible (J. E. W., pers. obsv.).

Distribution. Known only from Indonesia (Billard 1913) and Queensland (Bale 1884).

Family Kirchenpaueriidae Stechow, 1921**Genus Kirchenpaueria Jickeli, 1883*****Kirchenpaueria irregularis* Millard, 1958**

(Fig. 45A, B)

Kirchenpaueria irregularis Millard, 1958: 211.
- Millard 1975: 370. - Watson 1996: 79.

Kirchenpaueria sp. - Watson 1997: 530.

Record and material. NTM C13015, microslide, small infertile colony on oyster shell attached to boat mooring, Fannie Bay, near East Point, coll: K. Gowlett-Holmes, depth 3 m, 17/8/1998.

Description. Stems to 15 mm high, arising irregularly from a reptant hydrorhiza. Proximal stem region lightly fascicled, stems sparsely branched with one or two orders of branching. Cauline internodes long, narrow, smooth, nodes transverse to slightly oblique, prismatic of internodes thin; hydrocladia alternate, arching gracefully away from a short apophysis with transverse distal node. Hydrocladial internodes long, slender, smooth, nodes transverse to slightly oblique, no intranodal septa; most internodes thecate but some hydrocladia with an athecate segment. Hydrotheca on distal third of internode, cup-shaped, adcauline wall lying parallel to but free of internode; abcauline wall contiguous with internode, curving upwards; margin circular, rim faintly everted, perpendicular to hydrothecal axis and tilted proximally away from axis of internode. Nematothecae all of same size and shape, bithalamic, minute, mesial inferior distant from hydrotheca, mesial superior near distal node; one cauline nematotheca above axil of apophysis and one on internode below apophysis, a small mamelon on distal side of apophysis facing axillar nematotheca.

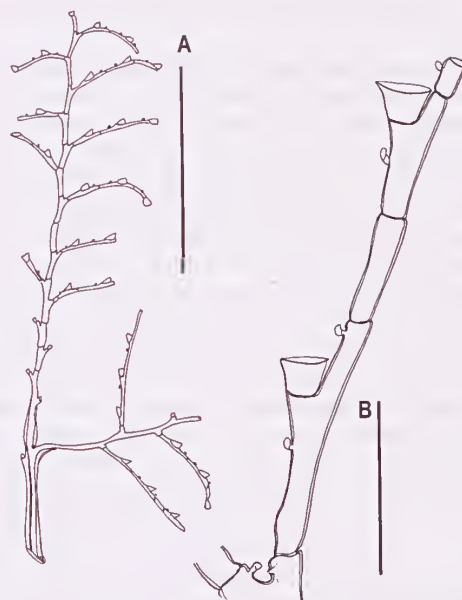


Fig. 45. *Kirchenpaueria irregularis*: A, stem from colony, East Point. B, hydrocladium. Scale bars: A, 3,000 μ m; B, 300 μ m.

Colour. Live colonies transparent white.

Measurements (μ m).**Stem**

length of internode	304 - 656
diameter at node	56 - 104
length of apophysis	40 - 56

Hydrocladium

length of thecate internode	400 - 544
diameter at node	36 - 48

Hydrotheca

length abcauline wall	44 - 68
diameter of marginal rim	76 - 96

Remarks. Colonies of this small species are fragile and lax, collapsing out of fluid. The specimens conform in all respects (including the irregular internode length and insertion of ancillary athecate internodes in the hydrocladium) with Millard's (1958, 1975) description and dimensions of the species.

Distribution. South Africa (Millard 1975). Australia; previously recorded from the Abrolhos Islands and Australian west coast Watson (1996, 1997).

Family Aglaopheniidae**Marktanner-Turneretscher, 1890****Genus Aglaopheuia Lamouroux, 1812*****Aglaopheuia delicatula* (Busk, 1852)**

(Fig 46A-E)

Plumularia delicatula Busk, 1852: 396.

Aglaophenia delicatula - Bale 1884: 167.

- Kirkpatrick 1890: 604. - Borradaile 1905: 843. - Billard 1913: 106. - Jäderholm 1920: 8. - Jarvis 1922: 350. - Pennycuik 1959: 185.

Thecocarpus delicatulus - Millard and Bouillon 1973: 94.

Records and material. NTM C13017, microslide, colony from Stn 81. NTM C12884, alcohol preserved material, colony from Stn 154. NTM C12883, alcohol preserved material; NTM C13020, MV F87897, microslides, colony from Stn 156. NTM C13019, microslide, colony from Stn 153. MV F86931, alcohol preserved material; NTM C13018, microslide, colony from Stn 127. NTM C13016, MV F86896, microslides, colony from Stn 40. Many infertile colonies, mostly on *Eunice tubifex*; one colony on stem of sertulariid hydroid. *Other records.* Stn 147, Plater Rock, colony on *Eunice tubifex*, coll: J. E. Watson, depths 3 - 10 m, 22/9/1999.

Description. Hydorrhiza knotted; stems to 35 mm high, plumose, monosiphonic, unbranched, narrowing distally, prosegment ahydrocladial, with strong distal hinge joint; stem thereafter hydrocladial. Hydrocladia frontal on stem, closely alternate, one on internode, cauline nodes transverse, indistinct or absent. Hydrocladial internodes short, nodes transverse, an intrathecal septum passing almost vertically downwards from posterior of hydrotheca to wall of internode opposite, a weak partial or complete septum passing from base of lateral nematotheca into internode. Hydrotheca conical, adcauline wall flatly convex, adnate, abcauline wall convex; a strong septum passing from abcauline wall to base, connecting with intranodal septum; margin dentate with a fairly long mesial abcauline cusp, an indentation at base of cusp opposite mesial nematotheca; mesial abcauline cusp flanked by a pair of blunt cusps, followed a more rounded pair, a third very low pair and sometimes a fourth posterior pair reduced to an mere undulation.

Mesial nematotheca tubular, free part short, not reaching hydrothecal margin, terminal orifice circular to canalliculate, an elliptical secondary orifice connecting with hydrotheca at base of free part; lateral nematotheca tubular, a little tumescent distally, bent forward beyond hydrothecal margin, orifice circular, only slightly excavated on adcauline side. Cauline nematothecae more or less bean-shaped, with a single orifice, one in axil, one of similar size below, both facing outwards and one larger, above hydrocladium.

Colour. Stems brown, hydrocladia almost white.

Measurements (µm).

Stem	
length of internode	224 - 232
width at node	84 - 88
Hydrocladium	
length of internode	212 - 228
width at node	64 - 84
Hydrotheca	
depth, mesial abcauline cusp to base	180 - 196
width of margin	120 - 128
Nematotheca	
length of mesial	200 - 212

diameter at orifice	18 - 26
length of lateral	104 - 112
diameter at orifice	20 - 24

Remarks. The specimens do not entirely conform with descriptions of *Aglaophenia delicatula* by Bale (1884) and Billard (1913). Billard gives a length of 340 - 380 µm and 40 - 50 µm for width of the hydrocladial internodes but these dimensions do not agree with an internode length of 110 µm calculated from his figure (Fig. 106). These dimensions differ considerably from both Bale's measurements (calculated from Pl. 14, Fig. 4) and those of the present specimens. Nor does the Beagle Gulf material agree with Bale's description of two cauline nematothecae below the hydrocladium, there being only one, centrally placed on the internode just above the node; Billard (1913) does not mention cauline nematothecae in his description. Despite these differences I have no doubt that the Beagle Gulf material is *A. delicatula*. The species may be an obligate epizooite of *Eunice tubifex*.

Distribution. Tropical northern and eastern Australia (Pennycuik 1959), Maldive Islands (Borradaile 1905).

Genus *Gymnangium* Hincks, 1874

***Gymnangium hians* (Busk, 1852)**

(Fig 47A-E)

Plumularia hians Busk, 1852: 396.

Halicornaria hians - Bale 1884: 179. - Kirkpatrick 1890: 604. - Stechow 1909: 101. - Stechow 1913: 10, 94. - Billard 1913: 68. - Jäderholm 1916: 8. - Briggs 1918: 47; - Stechow 1919: 425. - Bedot 1921: 347. - Jarvis 1922: 355. - Nutting 1927: 237. - Vervoort 1941: 222. - Millard 1958: 219. - Pennycuik 1959: 186.

Halicornaria haswelli Bale, 1884, 180.

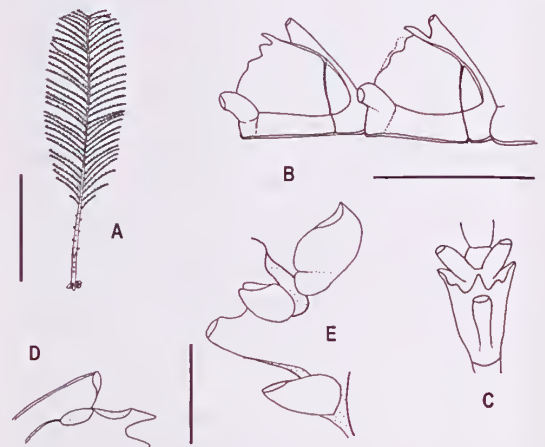


Fig. 46. *Aglaophenia delicatula*: A, stem from colony from Beagle Gulf. B, hydrocladial internode. C, hydrotheca, anterior view. D, mesial nematotheca. E, eauline nematothecae. Scale bars: A, 10 mm, B, C, D, 300 µm; E, 100 µm.

Aglaophenia balei Marktanner-Turneretscher, 1890: 272. - Billard 1905: 334.

Halicornaria balei - Ritchie 1910: 22.

Halicornaria flava Nutting, 1905: 955.

Halicornaria hians var. *laxa* Ritchie, 1910: 835.

Halicornaria hians var. *balei* Billard, 1913: 70. - Bedot 1921: 347. - Van Gernerden-Hoogveen 1965: 70.

Gymnangium hians - Stechow 1923: 19. - Stechow 1924: 69. - Stechow 1925: 254. - Yamada 1958: 51, 61. - Rees and Thursfield 1965: 171. - Millard and Bouillon 1973: 92. - Rho and Chang 1974: 147. - Millard 1975: 444. - Rho 1977: 279, 425. - Vervoort 1977: 84. - Vervoort and Vasseur 1977: 84. - Hirohito 1983: 77. - Ryland and Gibbons 1991: 542. - Hirohito 1995: 287. - Watson 1996: 79.

Gymnangium hians var. *balei* Mammen, 1967: 311. - Vervoort 1968: 114. - Schmidt 1972: 41. - Mergner and Wedler 1977: 24. - Van Praët 1979: 912.

Not *Gymnangium hians* - Jäderholm 1916: 8.

Records and material. NTM C12948, alcohol preserved material; NTM C13021, NTM C13022, MV F86928, fertile colony of five damaged stems detached from substrate, Stn 154. *Other records.* East Point, fertile colonies on *Eunice tubifex*, coll: J. E. Watson, depth 8 m, 17/8/1998. Plater Rock, many fertile colonies on *Eunice tubifex*, coll: J. E. Watson, depths 3-8 m 21/9/1999.

Description. Hydorrhiza ramified, stems unbranched, up to 40 mm long, stiffly plumose, monosiphonic, proximal stem wide, prosegment bearing remnant spurs

from shed hydrocladia; stem narrowing distally, perisarc thick and shining. Cauline nodes transverse, faint to distinct, hydrocladia alternate, on opposite sides of stem, directed upwards at an angle of c. 45° to axis, slightly recurved, usually two, sometimes one on internode; hydrocladia up to 20 mm long, internodes deep, nodes slightly oblique, faint, no intranodal septa. Hydrothecae saccate, contorted about middle, floor convex, proximal part of wall sometimes extended downwards into a knot of perisarc, free adcauline wall short, straight to slightly convex, abcauline wall completely adnate to mesial nematotheca, a thick hook-shaped intrathecal septum passing forward into hydrotheca from mid-abcauline wall, free end of septum a ragged edge (anterior view). Margin tilted upwards, a pair of sharply pointed, posteriorly pointing cusps in posterior third, margin strongly everted into pair of broad cusps, a pair of small cusps between lateral nematothecae, rarely a second pair of small, poorly defined cusps between these and lateral cusps.

Mesial nematotheca narrowing from base to apex, free part long, arching over hydrotheca, abcauline wall thickened, terminal orifice circular, a small secondary orifice just above junction with hydrotheca. Lateral nematothecae short, saccate, tubular, orifice large, open down to hydrothecal margin. Cauline nematothecae same as laterals, one above and one below hydrocladial apophysis and one behind axil.

Gonothecae conical, perisarc thin, in a single crowded row along stem, female containing a single planula larva.

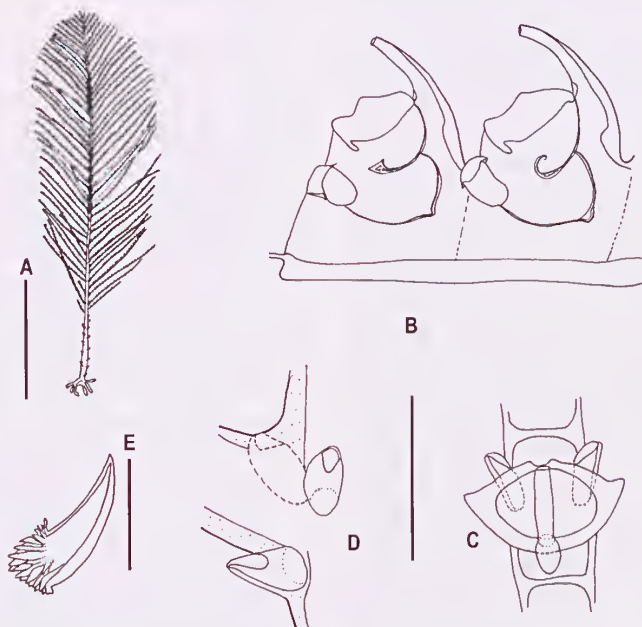


Fig. 47. *Gymnangium hians*: A, fertile stem from colony on *Eunice tubifex*, East Point reef. B, hydrocladial internodes. C, anterior view of hydrotheca. D, cauline nematothecae. E, intrathecal septum, showing ragged edge. Scale bars: A, 10 mm; B, C, D, 300 µm; E, 100 µm.

Colour. Stem shining dark brown, hydrocladia and gonothecae paler brown to cream.

Measurements (μm).

Hydrocladium	
length of internode	272 - 304
width of node	128 - 200
Hydrotheca	
depth, anterior margin to floor	180 - 200
width at margin (lateral view)	148 - 160
width across marginal lobes (top view)	268 - 288
Nematotheca	
mesial, length of free part	92 - 152
mesial, diameter of terminal orifice	16 - 18
lateral, length	84 - 100
Gonotheca	
length	900 - 1,000
width	520 - 680

Remarks. Ryland and Gibbons (1991) suggested a likely relationship of *Gymnangium haswelli* with *G. hians*. To investigate this, and relationships of *G. hians* with other similar Australian species I examined microslide preparations of putative type material of *Halicornaria haswelli* Bale, 1884 (MV F58843), *H. baileyi* Bale, 1884 (MV F58837) and *H. furcata* Bale, 1884 (MV F58839), held in the Museum of Victoria (see Stranks, 1993). *Gymnangium furcata* and *G. baileyi* from the temperate Australian east coast have similar branching habit and there are no microscopic characters that clearly differentiate them. *Gymnangium haswelli* and *G. hians*, known from subtropical and tropical Australia have unbranched plumose stems and also share similar microscopical characters. The four species thus fall into two distinct groups: *G. furcata* being conspecific with *G. baileyi*; and (supporting the suggestion of Ryland and Gibbons (1991)) *G. haswelli* is conspecific with *G. hians*. The Beagle Gulf and Darwin Harbour specimens conform exactly with the type of *G. hians* from Torres Strait.

It is possible that some of the many supposed variants of *Gymnangium hians* reported from the Indo-Pacific and other regions may be other, closely related species. For example, Bale's figure (1884, pl. 13, fig. 6) of the cuspidate hydrothecal margin of a specimen of *G. hians* exactly depicts the margin of a species, *G. undulatum*, described as new in this paper. *Gymnangium undulatum* can be clearly differentiated from *G. hians* by the long, undulated stems and cauline nematothecae. To establish the taxonomic limits of *G. hians* there is need for critical re-examination of preserved specimens of variants of the species reported from geographically different localities.

Gymnangium hians is one of the most abundant species in Darwin Harbour and environs, the colonies occurring almost exclusively on *Eunice tubifex*. It is surprising that the species was recovered from only one locality (Stn 154) in the wider Beagle Gulf survey.

Distribution. Type locality, Torres Strait. Known from tropical north-western Australia (Watson 1996) and Indo-Pacific (Ryland and Gibbons 1991, Watson 1996).

Gymnangium longicorne (Busk, 1852)

(Fig. 48A-F)

Plumularia longicornis Busk, 1852: 399.

Aglaophenia longicornis - Kirchenpauer 1872: 47. - Bale 1884: 157. - Bale 1886: 25. - Kirkpatrick 1890: 604. - Marktanner-Turneretscher 1890: 267.

Halicornaria longicornis - Billard 1913: 67. - Briggs and Gardner 1931: 195. - Pennycuik 1959: 186.

Halicornaria intermedia Billard, 1913: 65.

Halicornaria longicorne var. *sibogae* Billard, 1913: 67.

Lytocarpus longicornis - Bedot 1921: 315, 321.

Macrorhynchia longicornis - Stechow and Müller 1923: 474.

Macrorhynchia longicornia - Watson 1996: 79.

Records and material. NTM C12877, alcohol preserved material, colony from Stn 7. NTM C12878, alcohol preserved material colony from Stn 127. NTM C12879, alcohol preserved material; NTM C13025, NTM C13026, microslides, colony from Stn 87. NTM C13024, MV F 86916, microslides, colony from Stn 32. Large and small colonies, some fertile, on pebbles, bryozoans and ascidians. *Other records.* Stns 38, 40, 77, 78, 81, 91, 97, 104, 110, 129, 136, 137, 144, 147, 149, 150, 152, 156, 157, 159, 160. East Arm port channel, coll: J. E. Watson depth 4-6 m, 17/8/1998, Plater Rock, coll: J. E. Watson, depth 3-6 m, 21/9/1999, many large, fertile colonies on coral boulders and other invertebrate substrate.

Description. Hydromorpha a mass of tubular stolons entwining substrate, stolonial filaments passing up into strong cauline fascicular tubes. Stems to 3 mm in diameter at base and 190 mm long, plumose, prosegment ahydrocladate, unbranched. Branches of up to three orders given off in almost same plane from frontal tube of stem, ultimate branches monosiphonic, a long, blade-shaped hinge joint separating monosiphonic branches from preceding polysiphonic region, two short nematothecae on base of branch above joint. Branch internodes short, visible only in distal region, nodes transverse, distinct. Hydrocladium short, with up to six hydrothecae, borne on short apophysis on front of branch, hydrocladia alternate, crowded, recurved, two on internode; internodes short, node almost transverse, two strong, complete intranodal septa crossing internode, proximal one passing into hydrotheca as a partial intrathecal septum, distal node adjoining lateral nematotheca. Hydrotheca long, saccate, occupying entire internode, adcauline wall adnate to internode, abcauline wall convex posteriorly, free half of wall saddle-shaped and tilted upwards to margin, a deep wedge of perisarc passing into hydrotheca below margin. Margin parallel

with or inclined slightly to internode, a short mesial abcauline cusp connecting with perisarcal flange; margin circular with a pair of broad, centrally placed erect lateral lobes.

Mesial nematotheca very variable in length from very long, considerably overtopping hydrothecal margin to shorter than hydrothecal margin, length increasing distally along hydrocladium, longest nematothecae thin, tubular, sometimes a little swollen in distal third, terminal orifice small, circular, a larger secondary orifice on a short neck above hydrotheca and a small internal foramen connecting with hydrotheca. Shorter nematothecae with same terminal and secondary orifices as on longer nematothecae. Lateral nematotheca long, thin, tubular, sinuous, adnate to hydrotheca and extending beyond margin, terminal orifice circular. Two cauline nematothecae at hydrocladial apophysis, short, narrowing from base to small terminal orifice, proximal one pointing along hydrocladium, the other facing across branch.

Gonotheca inserted without pedicel in axil of hydrocladium, large, leaf-shaped at maturity, perisarc very thin, no terminal orifice, mature female gonophore with many small ova, not filling cavity.

Stem and branches bearing structures termed here "pseudophylactocarps" (see remarks) which usually replace the first or second hydrocladium on a branch; pseudophylactocarp long, lax, proximal two or three hydrothecae normal, followed by up to eight internodes each bearing two or three long, digitate nematothecae.

Colour. Live colonies dark grey-brown; preserved stems shining golden-brown, branches and hydrocladia paler brown.

Measurements (μm).

Hydrocladium	
length overall	1,200
length of internode	172 - 180
width at node	48 - 60
Hydrotheca	
depth, margin to floor	120 - 132
width at margin	76 - 80
Nematotheca	
mesial, free length (typical form)	180 - 220
mesial, diameter of terminal orifice	16 - 18
mesial, free length (intermedia form)	44 - 60
lateral, length	140 - 160
Gonotheca	
length	456 - 576
maximum width	160 - 272
pseudophylactocarp	
maximum length overall	1,900
length internode	180 - 200
length nematothecae	112 - 152

Remarks. Some morphological variants in the large sample of *Gymnangium longicorne* available for study conform with descriptions of *G. intermedium* (Billard 1913) and *G. longicorne* var. *sibogae* (Billard, 1913).

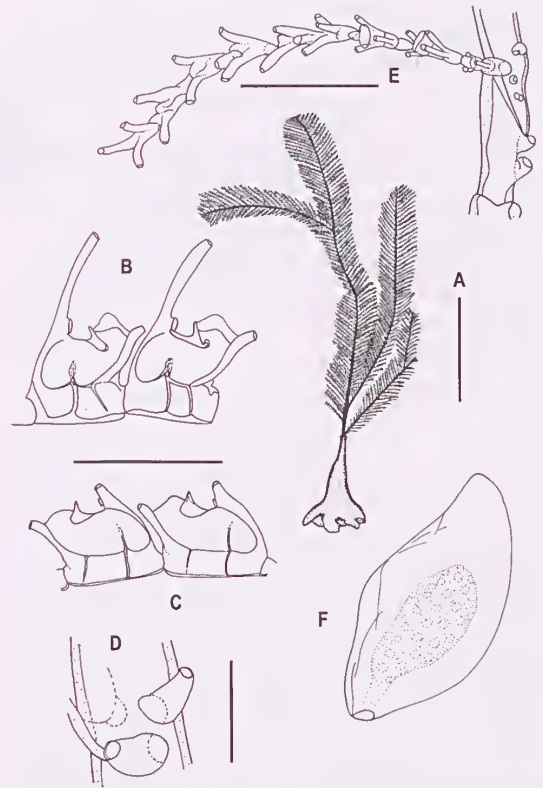


Fig. 48. *Gymnangium longicorne*: A, small colony from Beagle Gulf. B, hydrocladium with upwardly directed hydrothecae and long mesial nematothecae. C, hydrocladium from different colony from Beagle Gulf with parallel hydrothecae and short mesial nematothecae. D, cauline nematothecae. E, pseudophylactocarp from proximal stem region. F, female gonotheca. Scale bars: A, 50 mm; B, C, F, 300 μm ; D, 100 μm ; E, 500 μm .

Billard (1913) described and figured "hydroclades transformés" on the hydrocaulus of *Lytocarpia angulosa*. These lax and extremely flexible structures, present on several tropical species (J.E.W. pers. obsv.) are not true phylactocarps since they bear neither hydrothecae nor gonothecae and are defined here as "pseudophylactocarps". Lower stems of *G. longicorne* which are devoid of pseudophylactocarps are often invested with epizootic communities of small hydroids and other invertebrates but these epibionts are absent from regions where there are pseudophylactocarps. The nematothecae in the pseudophylactocarps are heavily armed, which, together with the sweeping action of these structures, is probably an adaptation to remove potential settlers from the stems. Hydrocladia and distal branches are quite deciduous, readily breaking off at hinge joints. Lateral nematothecae on distal parts of the hydrocladia are usually larger and more forwardly directed than those proximal on the hydrocladium.

Briggs and Gardner (1931) first described the gonotheca of *G. longicorne* from the Australian Great Barrier Reef. The range of developing and mature gonothecae in the present collection indicates that their material was immature.

Gymnangium longicorne is one of the most abundant hydroids in the Beagle Gulf collection and one of the more conspicuous species in Darwin Harbour.

Distribution. Indonesian region (Billard, 1913). Australian distribution: Torres Strait (Busk 1852), tropical Queensland (Pennycuik 1959). The locality of Port Jackson given by Marktanner-Turneretscher (1890) is probably incorrect.

Gymnangium undulatum sp. nov.
(Fig 49A-F)

Record and material. Holotype, NTM C12952, alcohol preserved material; NTM C13027, NTM C13048, MV F86901, microslides from holotype. Large colonies on top of coral boulders, Plater Rock coll: J. E. Watson, depth 4 m, 22/9/1999.

Description. Hydorrhiza composed of thick stolons reptant on substrate. Stems long, to 250 mm, plumose, unbranched, monosiphonic, strongly undulated, bends occurring every 15 - 25 mm along length, divided into internodes by strong, slightly oblique nodes, a tumescence below each node, cauline perisarc very thick, smooth. Prosegment ahydrocladate, in hydrocladate region, hydrocladia close, alternate, directed slightly forwards from opposite sides of stem on a moderately long apophysis with distal hinge joint; two, occasionally three, hydrocladia on internode, if two, proximal in lower third to halfway along internode, upper one just below distal node; sometimes two opposite hydrocladia and on internode. Hydrocladial nodes slightly oblique, marked only by a faint constriction and thinning of perisarc; no intranodal septa. Hydrothecae saccate, margin tilted obliquely backwards at an angle of c. 40° to hydrocladial axis, a strong septum passing forwards into body from midway along abcauline wall, septum dividing wall into two pronounced convexities, in ventral view septum seen as a shelf with ragged edge; adcauline hydrothecal wall gently convex, a small knot of perisarc at connection with internode. Hydrothecal margin with three pairs of equidistant, deeply scalloped cusps, no unpaired anterior tooth, cusp of middle pair the largest (lateral view), often pointing posteriorly; posterior cusp the broadest, posterior margin of hydrotheca straight between lateral nematothecae.

Mesial nematotheca digitate, just overtopping hydrothecal margin, terminal orifice may be entirely absent or with a small orifice on side facing hydrotheca, orifice just above hydrothecal margin or a completely open gutter from apex to hydrothecal margin. Lateral nematothecae small, rectangular to elongate conical, proximally rounded, distal end level with hydrocladium,

a large connection with internode and a large terminal orifice. Three cauline nematothecae associated with apophysis: two frontal, large, one in axil and one below apophysis, the one below with two large excavated orifices side by side, axillar one with a single orifice of similar shape, orifices facing distally; rear nematotheca behind axil, smaller, similar to laterals but with wider orifice, facing distally.

Colour. Live colonies grey-brown.

Measurements (µm).

Stem	
length of internode	576 - 1,088
diameter at node	240 - 304
Hydrocladium	
length of internode	280 - 336
width at node (lateral view)	120 - 152
Hydrotheca	
depth, marginal cusp to floor	240 - 304
width at margin	172 - 180
height of middle marginal cusp	44 - 68
Nematotheca	
mesial, free length	56 - 84
mesial, diameter of terminal orifice	
lateral, length	80 - 86
lateral, width at orifice	52 - 72
cauline, maximum length	128 - 140

Remarks. While there is no discernible change in size, shape or orientation of the cauline internodes at the bends in the hydrocaulus, at each bend the hydrocladia reverse their orientation, so that the group facing the front is succeeded by a rear-facing group.

Although the colonies are infertile, I have little doubt that the species should be referred to *Gymnangium*. Jäderholm (1916) briefly described *G. lians* (Busk, 1852) from a small specimen collected off Cape Jaubert, north-western Australia. His description and figure shows it to undoubtedly be *G. undulatum*. In microscopical characters, *G. undulatum* has much more deeply scalloped marginal cusps than *G. lians*. In the field, colonies of *G. undulatum* are unmistakable, growing in thick groups of undulating stems 300 - 400 mm high (extending to 500 - 600 mm when straightened out). *In situ*, the species can deliver a painful, long-lasting sting.

Gymnangium undulatum was found only at Plater Rock, where numerous large colonies occurred on upper surfaces of coral rock in good current flow at 3 - 4 m depth.

Etymology. Named for the tall, undulating stems.

Gymnangium unjuense sp. nov.
(Fig. 50A-E)

Record and material. Holotype, NTM C13023, NTM C13028, MV F86898, microslides, infertile colony from Stn 104. Paratype, NTM C13029, microslide, small infertile colony from Stn 110 (no preserved material remaining).

Description. Stems simple, plumose, to 50 mm high, arising from a thin, reptant hydorrhiza embedded in fine

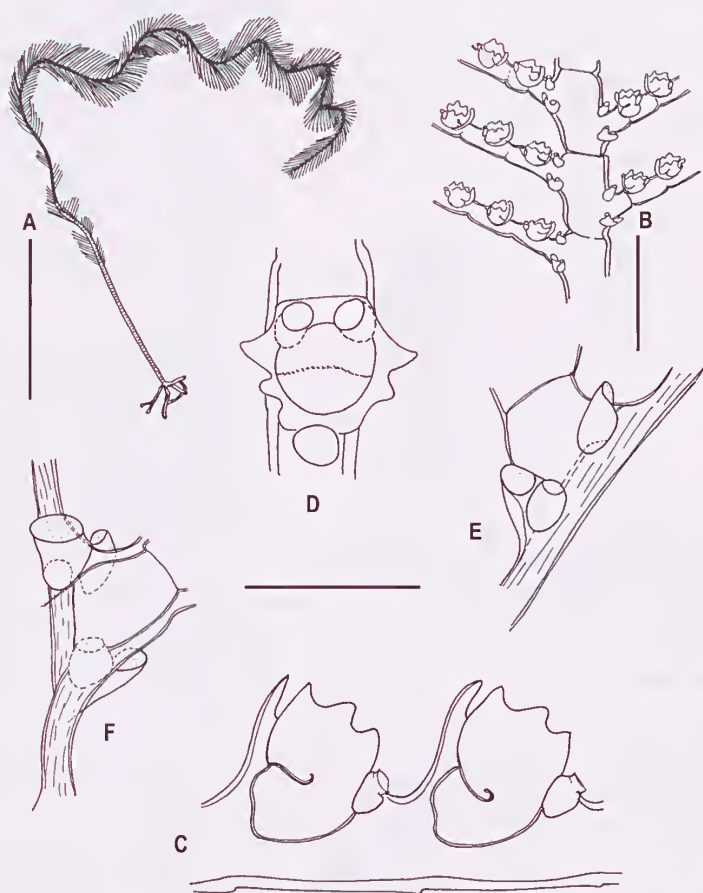


Fig. 49. *Gymnangium undulatum* sp. nov. A, stem from holotype colony from Plater Rock. B, hydrocladial part of stem. C, hydrocladial internodes. D, anterior view of hydrotheca. E, cauline nematothecae flanking apophysis, frontal view. F, cauline nematothecae, rear view. Scale bars: A, 50 mm, B, 1,000 µm; C-F, 300 µm.

sediment. Stem fascicled, prosegment consisting of many parallel tubes, becoming monosiphonic distally, perisarc thick; proximal stem ending in a pronounced blade-shaped hinge joint, blades connected by a thin web of perisarc. Entire length of fascicular tubes other than axillar tube with a row of closely spaced ovoid nematothecae; axillar tube unsegmented, giving off hydrocladia at an angle of c. 30° to axis. Hydrocladial apophysis short, distal node transverse, indistinct, internodes thereafter moderately long, perisarc smooth, thick, nodes merely a faint thinning of perisarc; three equidistant partial intranodal septa below hydrotheca, proximal septum short, mid-septum longer, curved forwards, distal septum straight or curved backwards from base of lateral nematotheca.

Hydrotheca entirely adnate to internode, body semi-ovoid, tilted upwards at an angle of c. 30° to internode, posterior adcauline wall deeply sunk in internode, a short plug-like extension of the middle intranodal septum

passing into hydrotheca from summit of an upward bulge in internode; abcauline wall weakly convex to sinuous, a slight concavity behind margin. Margin transverse to hydrothecal axis, mesial abcauline cusp prominent, sharply pointed, followed by three pairs of very shallow, scalloped cusps; margin straight between lateral nematothecae; perisarc of hydrotheca thin, thickening a little below margin.

Mesial nematotheca completely adnate to hydrotheca, terminating below margin, orifice sinuate, open down to hydrotheca; lateral nematotheca conical, widening to deep gutter-shaped orifice, open to internode. Cauline nematothecae same as laterals, orifice large, one above hydrocladium, facing upwards along stem axis and one below, facing along hydrocladium, a large circular mamelon between; nematothecae on polysiphonic tubes of stem ovoid.

Colour. Stem honey brown; hydrocladia lemon yellow.

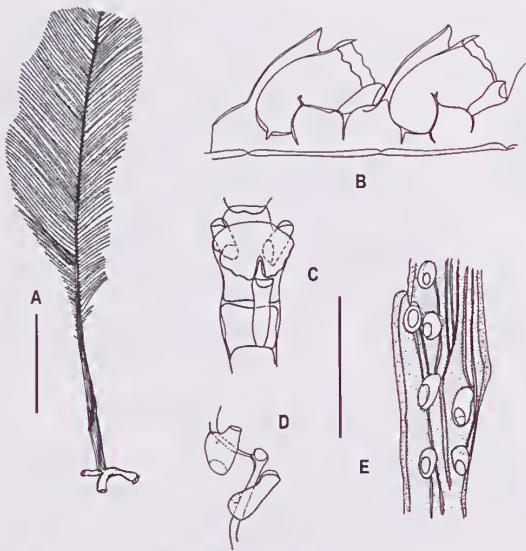


Fig. 50. *Gymnuangium unjinense* sp. nov. A, whole stem from holotype, Beagle Gulf. B, hydrocladium. C, anterior view of hydrotheca. D, cauline nematothecae. E, ovoid nematothecae on proximal stem. Scale bars: A, 10 mm, B-E, 300 µm.

Measurements (µm).

Stem	
width at base	1,000
diameter of axial tube	128 - 176
distance between hydrocladia on same side	600 - 624
Hydrocladial internode	
length	296 - 344
width at node	88 - 112
Hydrotheca	
axial length margin to base	216 - 240
diameter at margin (lateral view)	160 - 176
length mesial cusp (lateral view)	48 - 56
Nematotheca	
length mesial	232 - 272
height mesial apex above hydrotheca	44 - 52
length lateral	100 - 112
maximum width (lateral view)	44 - 52

Remarks. The distinctive ovoid cauline nematothecae appear as parallel series of closely spaced white dots in the ahydrocladial region of the stem. In some morphological features *Gymnuangium unjinense* is related to *Lytocarpia orientalis* (Billard, 1913); however it differs from that species in 1) absence of a mamelon from the base of the hydrocladium, 2) the hydrothecal margin has three, not four pairs of cusps and 3) in the well developed intranodal septa which are only incipient in *L. orientalis*. The species is only provisionally assigned to *Gymnuangium*. When fertile material is found, it may need to be transferred to another genus; if to *Lytocarpia*, then its relationship with *L. orientalis* will need to be re-examined.

Etymology. Named for the type locality off Unjin Point in the Beagle Gulf.

Genus *Lytocarpia* Kirchenpauer, 1872

Lytocarpia angulosa (Lamarck, 1816)

(Fig 51A-G)

Plumularia augulosa Lamarck, 1816: 126.

Aglaophenia angulosa - Lamouroux 1816: 166.

- Lamouroux 1924: 15

Plumularia huxleyi Busk, 1852: 395.

Thecocarpus angulosus - Billard 1913: 85.

Aglaophenia huxleyi - Bale 1884: 161. - Bale 1886: 26.

Acanthocladium huxleyi - Kirkpatrick 1890: 604.

Thecocarpus angulosus - Billard 1913: 85. - Briggs and Gardner 1931: 192.

Acanthocladium angulosum - Bedot 1921: 335.

- Stechow and Müller 1923: 476.

Records and material. NTM C12880, alcohol preserved material; NTM C13031, microslide, colony from Stn 126. NTM C12882, alcohol preserved material, colony from Stn 113. NTM C12881, alcohol preserved material; NTM C13030, microslide, colony from Stn 93. MV F86939, alcohol preserved material, colony from Stn 120. NTM C13032, MV F86917, microslides, colony from Stn 110. Infertile colonies on pebbles and shellgrit. *Other records.* Stns 17, 27, 66, 67, 77, 82, 87, 89, 92, 100, 104, 105, 106, 111, 114, 115, 116, 118, 119, 127, 132, 136, 152, 159, 160, 161. East Port channel bed, infertile colony on coarse sand, coll: J. E. Watson, depth 6 m, 20/9/1998.

Description. Hydrorhiza a bundle of thin, fibrous stolons; colonies of single, straight stems to 500 mm high and 2 mm wide at base, prosegment long, polysiphonic, ahydrocladial, comprising numerous parallel tubes, some running almost to tips of branches; upper stem region bearing single plumose hydrocladial branches to 30 mm long in verticels of three; branch internodes short, nodes oblique, faint. Hydrocladia alternate, long, close-set, inserted in front of frontal tube of branch, internodes short, nodes slightly oblique, distinct to absent; no intranodal septa. Hydrotheca irregularly hemispherical, anterior adcauline wall strongly convex, lower wall gently rounded, a concavity between two large knots of perisarc separating the two wall sections; a thick intrathecal septum passing from base of mesial nematotheca obliquely forward two thirds distance into hydrotheca, terminating in a knot of perisarc. Margin circular with a single, short mesial abcauline cusp connecting with intrathecal septum followed by three pairs of broad, low lobes, the first pair slightly more acute than others.

Mesial nematothecae of two distinct lengths on different colonies: long nematotheca tubular, arching over hydrothecal margin, terminal orifice small, excavated, base of nematotheca broad at junction with

hydrotheca, a secondary orifice, sometimes absent, just above hydrotheca, a small foramen connecting base with hydrotheca; short nematothecae may or may not overtop hydrothecal margin, base same as that of long nematotheca, orifice excavated, often connecting with secondary orifice above hydrotheca. Lateral nematotheca triangular, extending to and sometimes overlapping hydrocladial node; orifice broad, a small posterior foramen connecting with hydrocladium. Polysiphonic tubes of stem and branches with rows of oblong nematothecae, each with a single terminal orifice. Numerous pseudophylactocarps arising at intervals from the outermost polysiphonic tubes of stem and branches to just above first hydrocladium; pseudophylactocarps short, lax, comprising up to 20 short segments separated by deeply constricted nodes, each segment with three long, tubular nematothecae, terminal orifice of nematotheca sinuous, sometimes minutely crenulated; nematotheca containing a battery of large nematocysts.

Colour. Stems light brown, hydrocladia pale yellow-brown.

Measurements (μm).

Hydrocladium		
overall length	2,900	-3,000
length of internode	200	- 224
width at node	96	- 112
Hydrotheca		
depth	128	- 160
width at margin	136	- 144
Nematothecae		
length of short mesial	240	- 280
width of orifice, short mesial	28	- 32
length of long mesial	280	- 320
width of orifice, long mesial	32	
length of lateral	80	- 104
width of orifice, lateral	16	- 20
Pseudophylactocarp		
maximum length	2,500	
length of internode	160	- 180

Remarks. The present material conforms to the redescription of Lamarck's type material of *Plumularia angulosa* by Billard (1909).

There is no lengthening of the mesial nematothecae along the hydrocladium such as occurs in some aglaopheniid species, the long and short forms of nematothecae occurring on separate colonies, those with long mesial nematothecae being the more common form.

The tall, single stems growing from a large bundle of fibrous stolons are well adapted to life strong current flow in beds of tidal channels. *Lytocarpia angulosa* is one of the most abundant species in the Beagle Gulf collection. The structure and presumed purpose of pseudophylactocarps has been discussed previously.

Distribution. Indonesian region and Indian Ocean (Millard and Bouillon 1973), Australian tropical east coast (Pennycuik 1959).

Lytocarpia phyteuma (Kirchenpauer, 1876) (Fig. 52A-G)

Aglaophenia phyteuma Kirchenpauer, 1876: 23.

Aglaophenia clavacula Whitelegge, 1899: 373.

Thecocarpos phyteuma - Stechow 1919: 139.

-Pennycuik 1959: 187. - Millard and Bouillon 1973: 95.

?*Thecocarpos phyteuma* - Vervoort and Vasseur 1977: 86

Thecocarpos leopoldi Leloup, 1930: 1.

Lytocarpia phyteuma - Ryland and Gibbons 1991: 548.

Records and material. NTM C12953, alcohol preserved material; NTM C13033, NTM C13034, MV F86899, microslides, fertile colony on *Eunice tubifex*, Stn 154. NTM C13081, MV F86927, microslides, East Point, fertile colony on *Eunice tubifex*, coll: J. E. Watson, depth 7 m, 17/8/1998.

Description. Hydrorhiza tubular, entwining substrate. Stems plumose, to 50 mm high, unbranched, monosiphonic, prosegment ahydrocladial, divided thereafter into short internodes by indistinct transverse nodes, perisarc thick. Hydrocladia alternate, frontal on stem, close, one on internode, held out stiffly at an angle of c. 45°; hydrocladia long with up to 30 hydrothecae, first hydrothecate internode addressed to hydrocaulus, perisarc of internode thick, nodes marked by a notch and a faint transverse line or thinning of perisarc, a short intranodal septum passing from posterior of hydrotheca.

Hydrotheca semi-ovoid, a strong partial to entire septum passing from internode into hydrotheca at about one third distance from posterior margin; margin inclined backwards at c. 35° to internode, mesial abcauline cusp tongue-shaped, prominent, flanked by three pairs of rounded cusps of almost equal size and shape, not bent outwards and a pair of smaller, sharper cusps, bent slightly outwards behind lateral nematothecae. Perisarc of hydrotheca moderately thick, thinner below margin but thickened below marginal cusps.

Mesial nematotheca adnate to hydrotheca, not reaching hydrothecal margin, abcauline wall weakly convex to sinuous, narrowing to a gutter-shaped orifice open down to hydrotheca. Lateral nematothecae ovoid, facing outwards, narrowing distally, overlapping next internode, orifice large, gutter-shaped, open down to internode. Two nematothecae on each cauline internode, pouch-shaped with wide orifice, one just above node, the other at base of hydrocladium, facing outwards.

Corbula replacing a hydrocladium, proximal segment hydrothecate followed by an internode bearing a small, free leaflet; corbula with up to 20 ribs, corbula closed but with a distinct thinning of perisarc at base of ribs, free edges of ribs deep, upturned, no rachial internodes, base of each rib hydrothecate, margin of hydrotheca entire but without mesial or lateral nematothecae; rib with at least 12 erect nematothecae similar to hydrothecal

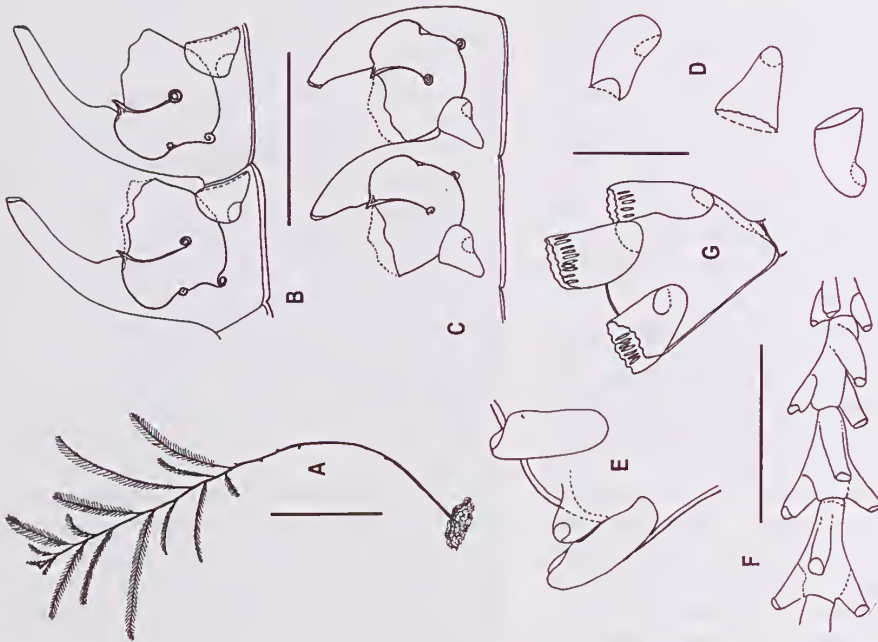


Fig. 51. *Lytocarpia angulosa*: A, colony from Beagle Gulf. B, hydrocladial internodes with long mesial nematothecae. C, hydrocladial internodes from different colony with short mesial nematothecae. D, lateral nematothecae from three angles of view. E, cauline nematothecae with central mamelon. F, part of pseudophyllactocarp from outer tubes of stem. G, pseudophyllactocarp nematothecae enlarged to show nematocysts. Scale bars: A, 50 mm; B, C, F, 300 μ m; D, E, G, 100 μ m.

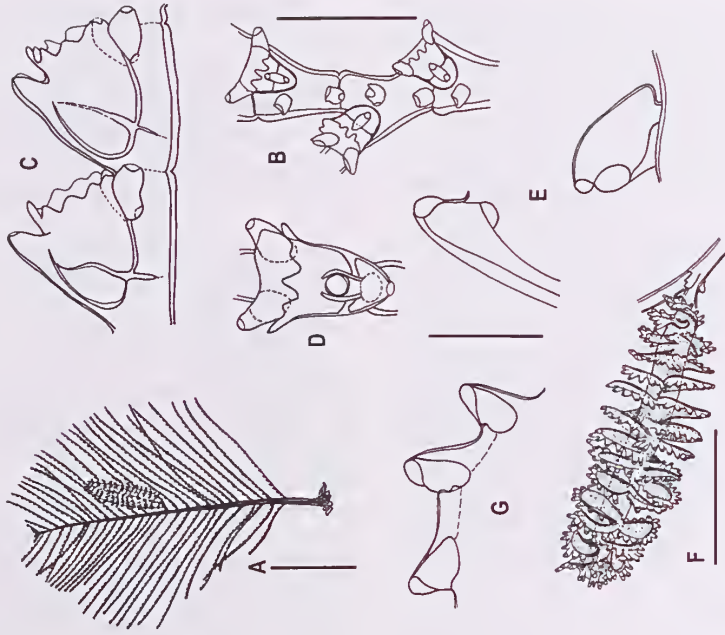


Fig. 52. *Lytocarpia phytiumia*: A, fertile colony from Beagle Gulf. B, stem and proximal hydrocladial internodes. C, hydrocladial internodes. D, anterior view of hydrotheca. E, mesial nematotheca. F, corbula. G, gonocladiol nematotheca. Scale bars: A, 5,000 μ m; B, 500 μ m; C, D, 200 μ m; E, 2,000 μ m; F, 1,000 μ m.

laterals, orifice of nematothecae wide, gutter-shaped. Gonophores probably female.

Colour. Stems deep honey brown, hydrocladia paler brown.

Measurements (μm).

Stem	
length of internode	304 - 344
width at node	128 - 144
Hydrocladium	
maximum length	12,000
Hydrocladial internode	
length	240 - 272
width at node	80 - 112
Hydrotheca	
length along base	218 - 224
depth, behind margin to base	136 - 144
width at margin	160 - 176
length of anterior marginal cusp	28 - 40
Nematothecae	
length of mesial	232 - 256
free height above hydrotheca	72
width of distal end (lateral view)	24 - 36
length of lateral	88 - 100
width at orifice (lateral view)	28 - 36
Corbula	
maximum length	6,000
width (lateral view)	1,120
height of leaflets above body	344 - 400

Remarks. Specimens from Beagle Gulf and Darwin Harbour generally conform to Stechow's (1919) description and figures of *Lytocarpia phyteuma*, however, the free part of the corbula ribs appear to be longer than shown by Stechow. The distinct partial hydrocladial intranodal septum described by Whitelegge (1899) for *A. clavacula* but not by Stechow is clear in the present specimens. There is some doubt that Vervoort and Vasseur's (1977) specimens from French Polynesia are indeed *L. phyteuma* because the hydrotheca shown in their fig. 36a is longer, lies parallel to the internode and the lateral nematothecae point downwards.

Colonies of *L. phyteuma* were found only on *Eunice tubifex*.

Distribution. Pacific region, tropical eastern Australia.

Genus *Macrorhynchia* Kirchenpauer, 1872

***Macrorhynchia philippina* Kirchenpauer, 1872**
(Fig. 53A-D)

Macrorhynchia philippina Kirchenpauer, 1872: 19. - Stechow 1923: 241. - Stechow and Müller 1923: 475. - Stechow 1924: 69. - Stechow 1925: 258. - Hirohito 1983: 78. - Rees and Vervoort 1987: 177. - Watson, 1996: 79. - Migotto 1996: 40. - Watson 1997: 538. - Calder 1997: 62.

Aglaophenia philippina - Kirchenpauer 1872: 29, 45-46.

Lytocarpus philippinus - Kirkpatrick 1890: 604. - Bale 1888: 786. - Billard 1913: 78. - Bale 1914: 6. - Bale 1915: 293. - Jäderholm 1916: 7. - Briggs and Gardner 1931: 193. - Millard 1958: 220. - Pennycuik 1959: 186. - Millard and Bouillon 1973: 93. - Millard 1975: 449.

Records and material. NTM C12894, alcohol preserved material; NTM C13036, microslide, colony from Stn 110. NTM C12893, alcohol preserved material; NTM C13037, microslide, colony from Stn 49. NTM C13035, microslide, colony from Stn 127. Large and small infertile colonies on *Eunice tubifex*. NTM C12895, MV F86936, alcohol preserved material, fertile colonies on other invertebrates and *Eunice tubifex* on wharf structures, Darwin Harbour, coll: J. E. Watson, depth 2-12 m, 17/8/1998. *Other records.* Stn 61. East Point, coll: J. E. Watson, depth 7 m, 19/8/1998. Plater Rock, colonies on other invertebrates and *Eunice tubifex*, coll: J. E. Watson depth 2-15 m 21/9/1999.

Description. Hydorhiza reptant on substrate. Colonies variable in size from single stems a few centimetres long to large complex colonies of several stems to 200 mm high. Stems erect, plumose, simple or branched, if branched, up to 4 mm wide at base, fascicled, polysiphonic tubes running parallel to near apex of branches. Two or three orders of branching may be present, branches straight, given off sparsely and irregularly from stem, branch internodes indistinct. Hydrocladia frontal on branch, alternate, one on internode; hydrocladial internodes short, deep, nodes slightly oblique; two partial intranodal septa, one passing

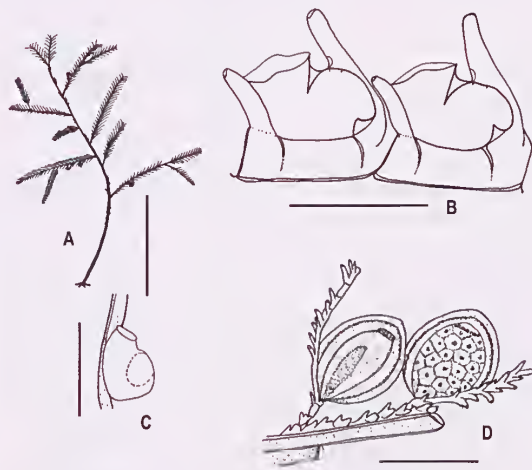


Fig. 53. *Macrorhynchia philippina*: A, small fertile colony from wharf pilings, Darwin Harbour. B, hydrocladial internodes. C, cauline nematotheca. D, phylactocarp with male and female gonothecae. Scale bars: A, 50 mm; B, 300 μm ; C, 100 μm ; D, 1,000 μm .

down from base of hydrotheca, the other from base of lateral nematotheca.

Hydrotheca saccate, adcauline wall flat or slightly convex in contact with internode, where free of internode attached to lateral nematotheca, a deep indentation in base at proximal end of adcauline wall, abcauline sinuate, rising abruptly behind margin, a deep V-shaped septum penetrating hydrotheca between mesial nematotheca and margin. Margin circular with a pair of opposite, low lobes.

Mesial nematotheca erect, tubular, parallel with hydrothecal abcauline wall, reaching to or beyond hydrothecal margin, tapering a little distally, terminal orifice circular, a little excavated on adcauline side, a secondary orifice above junction with hydrotheca and another, internal, connecting with hydrotheca. Lateral nematotheca long, tubular, inclined forward, overtopping hydrothecal margin, orifice circular or slightly excavated. A cauline nematotheca on branch at base of hydrocladium, short, body inflated, a circular orifice on a short neck.

Phylactocarp a modified hydrocladium given off from front of branch, phylactocarp about same length as gonotheca; proximal internode with a hydrotheca, next internode short, athecate, succeeding internode with two nematothecae and pedicel of gonotheca, following three to six internodes short with two long, digitate nematothecae with circular distal orifice. Gonothecae large, lenticular, containing a degenerate medusa, one or two gonothecae, sometimes a male and a female, on same rachis, perisarc thin, female containing many small ova. At release, medusa ovoid, without mouth or canals but with a ring of strongly refringent granules around margin.

Colour. In life, stems and branches dark brown to black, hydrocladia pale grey, male gonophore purple to black, female cream to pale orange. The refringent granules on the released medusa sparkle blue and white under the microscope.

Measurements (µm).

Hydrocladium		
maximum length		6,000
length of internode	280 -	320
width at node	64 -	88
Hydrotheca		
length along base	136 -	160
depth, margin to base	180 -	200
width across margin	160 -	180
Nematotheca		
maximum length of mesial	336 -	360
maximum free height	128	
width across orifice		20
length of lateral	160 -	168
width across orifice	20 -	22
Phylactocarp		
length	900 -	1,100
Gonotheca		
length	920 -	1,200

Nematotheca
length

120 - 176

Remarks. *Macrorhynchia philippina* is a very common tropical Australian species, colonies on the Great Barrier Reef growing to very large size (J. E. W., pers obsv.). Colonies on the polychaete *Eunice tubifex* in Beagle Gulf and Darwin Harbour were, however, quite small. Gonophores of the present material conform exactly with the description and figure of *M. philippina* by Gravier (1970). Other authors (see Calder 1997) have reported female gonophores containing one to three ova or planulae. Colonies of *M. philippina* can deliver a painful sting.

Distribution. Circumglobal tropical. Australian distribution: tropical Queensland to Western Australia (Pennycuik 1959, Watson 1997).

Macrorhynchia phoenicia (Busk, 1852) (Fig. 54A-E)

Plumularia phoenicia Busk, 1852:398.

Plumularia aurita Busk, 1852: 397.

Aglaophenia rostrata Kirchenpauer, 1872: 45.

Aglaophenia spectabilis Allman, 1883: 43.

Aglaophenia phoenicia - Bale 1884: 159. - Bale 1886: 15. - Bale 1887: 87. - Kirchenpauer 1892: 45. - Inaba 1892: 347.

Lytocarpus phoeniceus - Kirkpatrick 1890: 604. - Nutting 1905: 954. - Ritchie 1910: 21. - Billard 1910: 48. - 1913: 74. - Bale 1913: 138. - Stechow 1913: 95. - Jäderholm 1916: 7. - Jäderholm 1919: 25. - Jäderholm 1923: 5. - Bedot 1922: 181. - Jarvis 1922: 354. - Briggs and Gardner 1931:194. - Vervoort 1946: 328. - Pennycuik 1959: 187. - Millard 1968: 284. - Millard and Bouillon 1973: 94. - Millard 1975: 451: 94.

Lytocarpus phoenicea - Marktanner-Turneretscher 1890: 276. - Nutting 1927: 233. - Leloup 1930: 11.

Lytocarpus auritis - Bale 1913: 138.

Macrorhynchia phoenicia - Stechow 1921: 232. - Stechow 1923: 69. - Stechow 1925: 259. - Yamada 1959: 85. - Mammen 1965: 313. - Hirohito 1983: 80. - Ryland and Gibbons 1991: 555. - Hirohito 1995: 299. - Watson 1996: 79.

Records and material. NTM C12890, alcohol preserved material; NTM C13039, microslide, colony from Stn 136. NTM C12892, alcohol preserved material, colony from Stn 138. NTM C12891, alcohol preserved material, colony from Stn 7. NTM C13041, microslide, colony from Stn 156. NTM C13038, microslide, colony from Stn 137. Small unbranched colonies on *Eunice tubifex*; larger branched fertile colonies on calcareous bryozoans. MV F86935, alcohol preserved material, sparsely fertile colonies on *Eunice tubifex*, Plater Rock, coll: J. E. Watson, depth 12 m, 21/9/1999. *Other records.* Stns 127, 154. East Arm port site, many large colonies on rock and wharf structures, coll: J. E. Watson, depth 3-12 m, 20/9/1999.

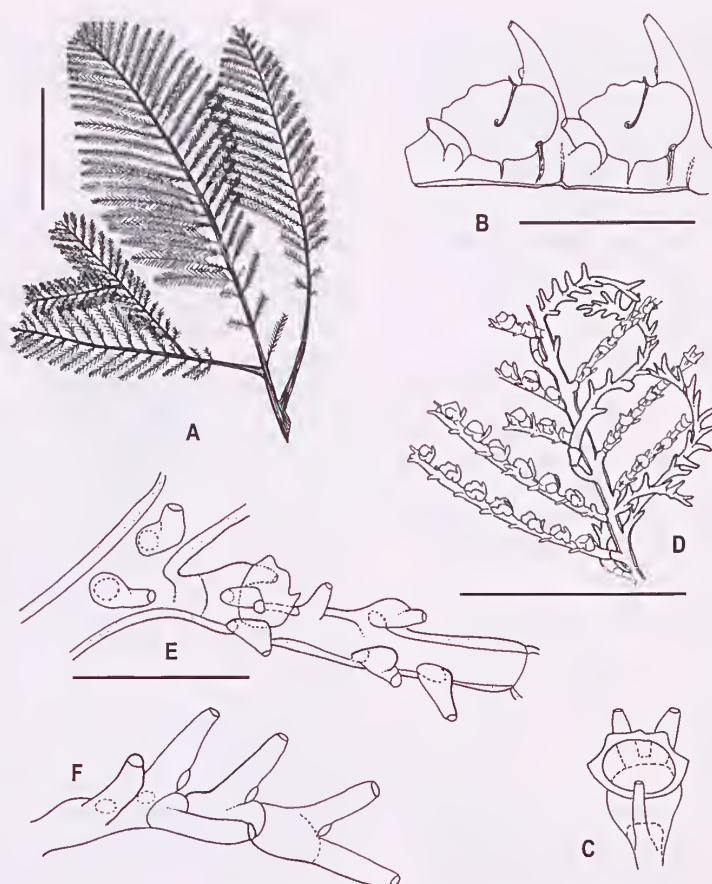


Fig. 54. *Macrorhynchia phoenicia*: A, branch from large colony from East Arm port, Darwin Harbour. B, hydrocladial internodes. C, hydrotheca, anterior view. D, phylactocarps on distal part of branch. E, proximal part of phylactocarp. F, distal part of phylactocarp. Scale bars: A, 10 mm; B, C, 300 µm; D, 3,000 µm; E, F, 500 µm.

Description. Colonies comprising three or four main stems arising from a tubular hydrorhiza entwining substrate. Tallest stems 200 mm, heavily fascicled, parallel polysiphonic tubes passing almost to tips of branches; branching fan-wise, primary branches given off from posterior axillar tube, secondary and tertiary branching common in large colonies. Branch prosegment with a long, blade-shaped distal hinge joint, nodes thereafter transverse, obscure, more distinct in monosiphonic distal region, perisarc of polysiphonic tubes thick, thinning distally. Hydrocladia alternate to subalternate, short, close, inserted on a cylindrical apophysis on axillar tube of branch; nodes transverse, internode with two strong partial to complete intranodal septa, the strongest near base of hydrotheca, the next, partial, beneath mid-adcauline wall, and two, weak, below walls of lateral nematotheca.

Hydrotheca short, ventricose, basal adcauline wall convex, distal part fused to lateral nematotheca, abcauline wall strongly convex, a short part free below

mesial nematotheca; body of hydrotheca divided by a strong, narrow, partial septum passing down into hydrotheca from free abcauline wall.

Margin tilted away from internode, mesial abcauline cusp a small spine connecting with intrathecal septum; margin subcircular, strongly everted, a pair of blunt cusps in mid-lateral region, a smaller pair near base of lateral nematothecae, a single, minute adcauline cusp between lateral nematothecae.

Mesial nematotheca moderately long, erect, tubular, tapering, usually considerably overtopping hydrothecal margin; abcauline wall convex, terminal orifice small, circular, a secondary orifice above junction with hydrotheca; lateral nematotheca tubular, bent, narrowing to margin, overlapping hydrocladial node, terminal orifice small, circular, a large oval foramen connecting with hydrotheca. Two cauline nematothecae at base of hydrocladium, tubular, shorter than laterals, body twisted, orifice circular, proximal nematotheca pointing along hydrocladium, distal one facing along branch.

Phylactocarp replacing proximal hydrocladium on branch; rachis long, arching, proximal internode with normal hydrotheca, next internode long with an oblique distal node and three short nematothecae similar to caulines; succeeding internodes with two or three digitate nematothecae like mesials, terminal orifice circular, a secondary orifice at base and a small internal foramen connecting with internode.

Colour. Live colonies uniform golden brown to dark brown.

Measurements (μm).

Branch (monosiphonic region)		
distance between hydrocladia on same side	376	- 480
Hydrocladium		
length of internode	256	- 264
width at node	64	- 80
Hydrotheca		
depth, floor to margin	136	- 140
width at margin	128	- 132
Nematotheca		
length of mesial	200	- 220
width of terminal orifice	16	- 18
length of lateral	100	- 112
Phylactocarp		
maximum length, mature	1,400	- 2,000
length of internode	140	- 156
length of abcauline wall of nematotheca	200	- 196

Remarks. The apical branches of larger colonies sometimes end in long, tangled tendrils. *Macrorhynchia phoenicia* is easily recognised by its bristly appearance, pinnate branching and uniformly brown colour. Short, immature colonies occur in habitat such as wharf structures and on *Eunice tubifex* while larger, presumably older, colonies occur in less disturbed habitat of natural reefs. It is very abundant in Darwin Harbour and probably more abundant in Beagle Gulf than suggested by the survey data.

Distribution. Tropical Indian Ocean, Indonesia, Japan (Millard 1975). Australian distribution: Torres Strait (Busk 1852), tropical Queensland (Pennycuik 1959).

Macrorhynchia ambigua sp. nov.

(Fig. 55A-G)

Records and material. Holotype, NTM C12960, alcohol preserved material, NTM C13080, NTM C13046, microslides from holotype; colony detached from substrate, Stn 154. Paratype, MV F86929, microslide, colony from wharf piles, Port of Darwin, on *Eunice tubifex*, coll: J. E. Watson, 5 m, 20/8/1998.

Description. Hydorrhiza a knot of tough stolons entwining substrate. Stems stiff, to 100 mm high, heavily fasciated, single stems branched irregularly alternate to subopposite, or stems may be branched fan-wise from hydorrhiza, secondary branching rare; polysiphonic tubes

of stem parallel, running along branches, but distal part of branches monosiphonic; nodes if present, transverse, prosegment ahydrocladial with a central row of nematothecae or oval foramen representing former sites of cauline nematothecae.

Hydrocladia frontal on axial tubes of stem and branches, short, alternate one per internode, inserted on apophysis with transverse to slightly oblique distal node and a reduced, central nematotheca. Hydrocladial internodes short, nodes transverse, indistinct, marked by a notch in perisarc; internode with two strong septa, one almost vertical below intrathecal septum, the other sloping distally from base of lateral nematotheca.

Hydrothecae not immersed in internode, ventricose, abcauline wall and proximal adcauline wall strongly convex, base flatter, posterior adcauline wall free of internode, a slightly oblique intrathecal septum passing almost halfway into hydrotheca from proximal intranodal septum. Margin inclined at an angle of 10 - 20° to internode with a prominent, blunt abcauline cusp passing downward into hydrotheca as a wide hatchet-shaped wedge; margin with a pair of low, central lobes, sometimes reduced to mere undulations, in frontal view, margin oval with smoothly everted rim, perisarc of margin very thin.

Mesial nematotheca reaching abcauline cusp, usually completely adnate, widening to orifice but with a short narrow neck seen only in frontal view. Lateral nematotheca on proximal hydrocladial internodes fairly short, lengthening a little distally along internode, tubular, reaching node but not reaching hydrothecal margin, orifice circular, connection with internode large. A cauline nematotheca at base of hydrocladial apophysis, small, like proximal hydrocladial laterals but with shorter orifice, facing upwards and outwards. Two large, tubular cauline nematothecae flanking hydrocladium, terminal orifice deeply excavated, a tumid mamelon with circular orifice between.

Phylactocarp replacing a branch hydrocladium, borne on a short apophysis, adcauline wall of basal internode with a reduced nematotheca; next internode long, upwardly curved below an unmodified hydrotheca, followed by a long internode with hydrotheca with twin lateral nematothecae and slightly reduced mesial nematotheca, a single long nematotheca similar to laterals above; phylactocarp thereafter directed upwards almost parallel to axis of branch, bearing up to eight internodes, nodes transverse, with two (sometimes one or three) opposite nematothecae. Nematothecae short, stubby, widest about middle, terminal orifice circular, a pore without collar at junction with internode. A single gonotheca borne frontally on a short pedicel on second hydrothecal internode, gonotheca large, lenticular, perisarc very thin and transparent, gonophore female, packed with small ova.

Colour. Live colonies brown, gonophore cream.



Fig. 55. *Macrorhynchia ambigua* sp. nov. A, holotype colony from Beagle Gulf. B, branch from larger paratype colony from wharf piles, Port of Darwin. C, part of stem with cauline nematothecae and hydrocladia. D, hydrocladial internodes. E, anterior view of hydrotheca. F, cauline nematotheca, frontal view with tumid mamelon on apophysis. G, phylactocarp with gonotheca. Scale bars: A, B, 50 mm; C, G, 500 µm; D - F, 300 µm.

Measurements (µm).

Branch (monosiphonic region)	
length of internode	200 - 272
width at node	136 - 160
length of apophysis, adcauline side	120 - 144
Hydrocladium	
maximum length of hydrocladium	1,900 - 2,100
length of internode	240 - 272
width at node	72 - 80
Hydrotheca	
length parallel to internode	216 - 240
depth, floor to margin	172 - 180
width at margin	132 - 140
length of abcauline cusp	32 - 40
Nematotheca	
length of mesial	192 - 212
width of terminal orifice	20 - 30
length of lateral	92 - 100
Phylactocarp	
overall length, mature	1,760 - 1,850

length of internode	140 - 160
width of node	72 - 100
length of abcauline wall	
of nematotheca	144 - 160
width of terminal orifice	44 - 48

Remarks. Some colonies show a tendency towards elongation of the mesial and lateral nematothecae along the hydrocladium; this may also be accompanied by slight exaggeration of the central (lateral) cusp on the hydrothecal margin in which case the hydrothecae show some resemblance to those of *Macrorhynchia philippina*. However, the reproductive structures, habit and colour of the colonies readily distinguish *M. ambigua* from *M. philippina*. In many respects *M. ambigua* also resembles *M. phoenicia*, and as the species share the same habitat, sterile colonies of *M. ambigua* can be easily mistaken for a variant of *M. phoenicia*; in fact it is likely that many so-called variants of *M. phoenicia* are actually *M. ambigua*. Reliable differences between the two species

are: 1) the intrathecal septum of *M. ambigua* is much wider in lateral view and more wedge-shaped than that of *M. phoenicia*, 2) the mesial nematotheca of *M. ambigua* is shorter than that of *M. phoenicia* and is completely adnate to the abcauline wall of the hydrotheca, 3) the mature phylactocarp differs significantly from that of *M. phoenicia* and 4) mature colonies of *M. ambigua* are much smaller and of paler brown colour than those of *M. phoenicia*.

The stems of *M. ambigua* are rather brittle, showing repeated regeneration after breakage above the hydrorhiza. It may be a sparingly fertile species, there being relatively few gonangia in the material examined. *M. ambigua* was found only on tubes *Eunice tubifex*. The bases of the stems are frequently overgrown by pale, soft sponge.

Etymology. Refers to the difficulty in distinguishing the species from *M. phoenicia*.

***Macrorhynchia quadriarmata* sp. nov.**

(Fig 56A-G)

Record and material. Holotype, NTM C13043, microslide, fragment of branched, infertile colony on shellgrit from Stn 137. (No preserved material remaining).

Description. Hydrorhiza of a few fragmentary stolons. Colony 30 mm high, stem lightly fascicled, polysiphonic tubes running almost to broken tip of stem; prosegment long, lowest two branches broken off, a hinge joint overgrown by fasciculations above stump of proximal branch; six remaining branches regularly alternate, distant, directed upwards, perisarc firm; frontal tube of caulus hydrocladate. Branches monosiphonic, borne on a long apophysis, distal node of apophysis transverse, followed by an athecate internode with a long blade-shaped distal joint, the two sections joined by a thin membrane, branch nodes thereafter transverse, narrow, obscure proximally, becoming more pronounced distally. Hydrocladia alternate, frontal on stem and branches, one, sometimes two on branch internode, inserted on a short apophysis with slender, acute distal node, hydrocladia bearing up to six hydrothecae, internodes rather long, nodes transverse, deeply constricted, base of internode curving from node below hydrotheca; two distinct, complete, almost vertical intranodal septa, one at proximal third of hydrotheca and one below lateral nematotheca.

Hydrotheca slipper-shaped, adcauline wall flat, bisected by an inclined, almost complete intrathecal septum connecting with intranodal septum, a small proximal foramen in base of wall usually obscured by tissue, abcauline wall convex to base of mesial nematotheca then recurving to margin, a deep pocket of perisarc behind margin. Margin almost parallel with internodal axis with a pair of broad, sometimes

proximally displaced lateral lobes; lobes everted, a small, blunt cusp between lateral nematothecae. Perisarc of hydrocladia and hydrothecae thin.

Mesial nematotheca erect, increasing in length distally along hydrocladium, proximal nematotheca on hydrocladium not reaching hydrothecal margin, distalmost nematotheca very long, thin, tubular, considerably overtopping hydrothecal margin, distal end swollen, terminal orifice of both forms small, circular, a large secondary orifice on a short neck above junction with hydrotheca. Lateral nematothecae bifid, superior nematotheca long, thin, tubular, sinuous, extending beyond hydrothecal margin, terminal orifice circular, inferior nematotheca tubular, much shorter and wider than superior, pointing obliquely downwards from internode; openings of both nematothecae to internode confluent through a small foramen.

Branch apophysis with one large cowl-shaped adcauline nematotheca, a similar nematotheca on succeeding athecate internode; orifice small, circular, facing downwards to internode, both nematothecae with a large foramen connecting with branch. A cauline nematotheca on branch at base of hydrocladium, large, like inferior lateral, pointing away from hydrocladium; nematothecae also present on axillar tube of stem above proximal hinge joint.

Pseudophylactocarps replacing first hydrocladium on lowest branches, rachis unbranched, first two or three internodes with normal hydrothecae followed by up to six internodes with long, tubular nematothecae similar to superior laterals, pointing obliquely forwards and outwards, terminal orifice circular, a secondary orifice just above base.

Colour. Honey brown.

Measurements (μm).

Stem		
width at base		168
distal width		152
distance between		
opposite hydrocladia	1,100	-1,560
Branch		
length of adcauline wall of apophysis	112	- 160
width of apophysis at node	88	- 104
length of abcauline wall		
athecate internode	320	- 440
Hydrocladium		
maximum length		1,400
length of apophysis	88	- 92
length of internode	224	- 248
width at node	28	- 32
Hydrotheca		
length of fixed adcauline wall	200	- 216
height, margin to base	128	- 160
width at margin	64	- 72
Mesial nematotheca		
free length	144	- 140

diameter of terminal orifice	12 - 16	height of cusp	32 - 60
width of secondary orifice	32 - 48	distance between cusps	48 - 68
Nematotheca		Gonotheca	
length of superior lateral	100 - 112	length, base to apex	420
diameter of terminal orifice	12 - 16	maximum width	170
length of inferior lateral	48 - 56	Remarks. Because of thinning of the marginal	
diameter of terminal orifice	16 - 20	perisarc it is difficult to accurately count the number of	
Phylactocarp		cusps in the few undamaged hydrothecae in the sample.	
length of nematothecate internode	168 - 176	The hydrothecae are smaller than descriptions of <i>Clytia</i>	
length of nematotheca	112 - 136	<i>warreni</i> , the number of marginal cusps variable and the	
Remarks. Several features characterise <i>Macro-</i>		two immature gonothecae do not show the distal	
<i>rhynchia quadriarmata</i> : 1) the small size and graceful		narrowing as reported for that species. The material is	
habit of the colony which is more like that of a		therefore referred with some doubt to <i>C. warreni</i> .	
plumulariid than an aglaopheniid hydroid, 2) the		Distribution. This is the first record of <i>C. warreni</i>	
exceptionally long mesial nematothecae, 3) the bifid		outside South Africa.	
lateral nematothecae and 4) the long blade-shaped			
proximal hinge joint of the branch with thin connecting			
membrane.			
Etymology. Named for the four lateral nematothecae			
on the hydrocladial internode.			
Family Campanulariidae Johnston, 1837			
Genus <i>Clytia</i> Lamouroux, 1812			
<i>Clytia</i> ?<i>warreni</i> Stechow, 1919			
(Fig. 57A-C)			
<i>Clytia elongata</i> Warren, 1908: 338 [<i>nomen nudum</i>].		<i>Clytia linearis</i> (Thornely, 1900)	
<i>Clytia warreni</i> Stechow, 1919: 48. - Millard 1975:		(Fig. 57D, E)	
221.			
Record and material. NTM C12946, alcohol		<i>Obelia linearis</i> Thornely, 1900: 453.	
preserved material; NTM C13044, MV F86886,		<i>Campanularia gravieri</i> Billard, 1904: 482. - Millard	
microslides, sparsely fertile colony on stem of <i>Pennaria</i>		and Bouillon 1973: 51. - Millard 1975: 215.	
<i>disticha</i> , Stn 87.		<i>Campanularia obliqua</i> Clarke, 1907: 9.	
Description. Hydrorhiza tubular, reptant on substrate.		<i>Clytia linearis</i> - Cornelius 1982: 84. - Gibbons and	
Hydrothecal pedicels variable in length, simple, perisarc		Ryland 1989: 404. - Calder 1991: 62. - Migotto 1996:	
smooth, hyaline, with up to eight proximal and eight		85.	
distal close annulations, sometimes a few annulations		Record and material. NTM C12945, alcohol	
mid-way along pedicel. Hydrothecae long, slender, sub-		preserved material; NTM C13045, MV F86887,	
cylindrical, widening above diaphragm in proximal third		microslides, small fertile colony on <i>Pennaria disticha</i> ,	
and just below margin, diaphragm distinct. Hydrothecal		Stn. 56.	
perisarc thinning distally; margin with six to 10 long,		Description. Hydrorhiza reptant on substrate. Single	
obtuse cusps, a deep embayment between, cusps often		hydrothecae and erect stems to 10 mm given off	
inclined inwards.		irregularly from hydrorhiza; stems monosiphonic,	
Gonotheca long, obconical, borne on an annulated		subsympodially branched; stem and branch internodes	
pedicel arising from the hydrorhiza, distal end truncate,		long, smooth, nodes a series of annulations. Hydrotheca	
orifice circular, closed by a sheet of tissue; perisarc of		distal on internode, one, sometimes two on internode,	
gonotheca thin and smooth.		pedicel short, annulated proximally and distally or	
Colour. Colourless.		completely throughout; hydrotheca slender, deeply	
Measurements (µm).		campanulate, expanding smoothly to margin, diaphragm	
Hydrorhiza, diameter	48 - 56	distinct, transverse, in empty hydrothecae marked by a	
Stem		ring of thorn-shaped desmocytes pointing into hydro-	
length	424 - 1,120	theca. Margin denticulate with 10 - 12 long, sharp cusps	
diameter	40 - 64	separated by deep embayments; perisarc thinning trough	
Hydrotheca		hydrotheca to become almost invisible at margin.	
length, base to apex of cusp	448 - 496	Hydranth with 14 - 16 tentacles.	
diameter at diaphragm	64	Gonotheca borne on an annulated pedicel in fork of	
diameter below marginal cusps	136 - 224	stem beside a hydrothecal pedicel; gonotheca long,	
		obconical, distally truncate, perisarc thin, enclosing up	
		to eight developing medusae, distal end of gonotheca	
		closed by a thin sheet of tissue; mature medusa (at point	
		of release) with 14 tentacles and inverted exumbrella.	
		Colour. White.	
		Measurements (µm).	
		Stem	
		diameter at base of erect stem	84 - 88
		length of stem internode	520 - 672

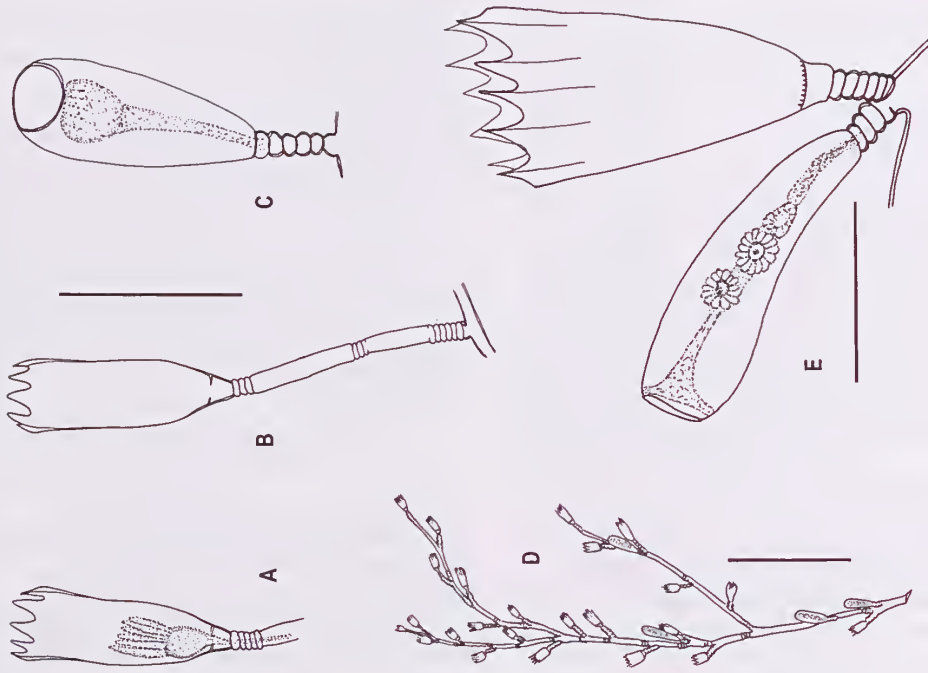


Fig. 57. A-C, *Clytia warreni*: A, B, hydrothecae from colony from Beagle Gulf. C, gonotheca from same colony. D, E, *Clytia linearis*: D, colony from Beagle Gulf. E, hydrotheca and gonotheca from same colony. Scale bars: A - C, E, 300 μm; D, 1,000 μm.

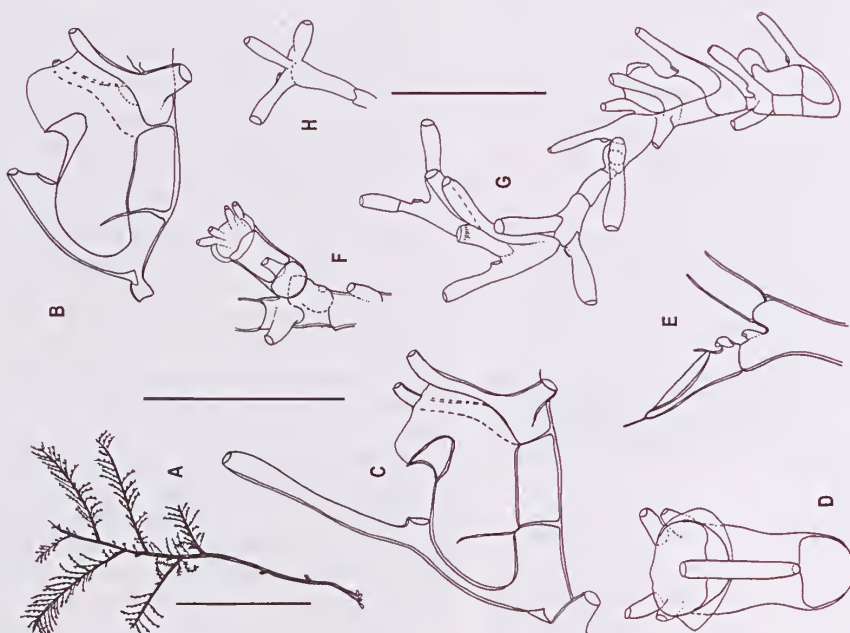


Fig. 56. *Macrorhynchia quadriarmata* sp. nov. A, holotype colony from Beagle Gulf. B, hydrotheca with truncated mesial nematotheca. C, hydrotheca with elongate mesial nematotheca. D, anterior view of hydrotheca. E, apophysis of stem with proximal hydrocladial internode and oblique hinge joint. F, cauline nematotheca. G, phylactocarp. H, distal end of phylactocarp with three nematothecae. Scale bars: A, 10 mm; B, C, D, 200 μm; E - H, 300 μm.

length of hydrothecal pedicel	200 - 880
diameter annulated hydrothecal pedicel	48 - 64

Hydrotheca

length, diaphragm to margin	624
diameter at diaphragm	72 - 100
diameter at margin	336

Gonotheca

length, excluding pedicel	488 - 640
distal diameter	120 - 200

Remarks. The specimens agree with dimensions of *C. linearis* given by Gibbons and Ryland (1989) and Migotto (1996). The perisarc is so frail that most hydrothecae collapse in mountant. The slight narrowing behind the distal end of the gonotheca shown by some authors (e.g. Gibbons and Ryland 1989, Migotto 1996) is not evident in the present material. There is a remarkable range in size of hydrothecae and if intergradations were not present on the same stem the extremes in size could be easily mistaken for two different species. The figured hydrotheca (Fig. 57E) was one of the largest found on the colonies.

Distribution. Tropical to warm temperate oceans and Fiji (Gibbons and Ryland 1989), Brazil (Migotto 1996). Not previously recorded from Australia.

***Clytia* sp. 1**

Record and material. Infertile colony on aglaopheniid hydroid, Stn. 61.

Remarks. The few remaining hydrothecae are too badly crushed for identification.

***Clytia* sp. 2**

Record and material. Infertile colony on bryozoan, Stn. 38.

Remarks. Stems simple, unbranched, annulated proximally and distally but the few remaining campanulate hydrothecae are crushed beyond recognition.

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Aceeped 14 November 2000

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The rediscovery of *Leandrites stenopus* Holthuis, 1950 (Crustacea: Palaemoninae), from Lucinda, Queensland

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ABSTRACT

A second specimen of the rare palaemonid shrimp *Leandrites stenopus* Holthuis, 1950, has been collected from Lucinda harbour, northern Queensland. The only previous specimen was collected on the Siboga Expedition in 1899, from Madura, Indonesia. This male specimen enables the generic placement to be confirmed and the geographic distribution to be considerably extended.

KEYWORDS: *Leandrites stenopus*, Crustacea, Palaemoninae, rediscovery, Queensland.

INTRODUCTION

The unique specimen of the small marine shrimp *Leandrites stenopus* Holthuis was collected in 1899 but was not described until 1950, half a century later. A further half century has elapsed before a second specimen was obtained. Despite innumerable marine faunistic surveys in tropical Indo-West Pacific waters during the last half century, it is still surprising that a species can remain so apparently rare. The present specimen was obtained during the course of a survey of the marine faunas of northern Queensland harbours carried out by the Department of Marine Biology and Aquaculture of James Cook University of North Queensland for Ports Corporation Queensland.

Abbreviations used: CL, post-orbital carapace length; NTM, Northern Territory Museum, Darwin.

SYSTEMATICS

Leandrites stenopus Holthuis, 1950

(Figs 1-3)

Leandrites stenopus Holthuis, 1950: 40-42, fig. 6. - Chace and Bruce 1993: 7-8.

Material examined. 1♂, Lucinda, stn Sh 62, 18° 31' S, 148° 19' E, 7 July-1999, modified Ockelman sled, 15 m, coll. F. Hoedt, NTM Cr.012794.

Description. In poor condition, lacking both second pereopods and some other appendages.

Rostrum (Fig. 1A) about 0.95 of CL, slightly exceeding antennular peduncle, exceeded by scaphocerite, acute, tapering, horizontal, feebly developed lateral carinae, with 11 acute teeth dorsally, first tooth

epigastric, second also situated on carapace, four small ventral teeth distally, numerous median sparsely plumose interdental setae dorsally, similar submedian marginal setae ventrally; inferior orbital angle (Fig. 3B) well developed, rounded, antennal spine lower, slightly submarginal, branchiostegal suture absent, branchiostegal spine similar to antennal, distinctly postmarginal, pterygostomial angle rounded, sparsely setose.

Ophthalmic somite without bec ocellaire, with small pigment spot.

Eye (Fig. 1D) with large globular cornea, diameter about 0.25 of CL, feebly pigmented, with accessory pigment spot, stalk about 0.8 of corneal width, slightly longer than wide.

Antennule (Fig. 1B) with proximal segment of peduncle twice as long as width, distolateral angle produced, rounded, with small acute distolateral tooth, stylocerite acute, short, not reaching half segment length, ventromedial border with small acute tooth at half length, statocyst well developed, with large circular statolith; intermediate and distal segments very obliquely articulated, subequal in length; upper flagellum biramous, proximal 5 segments of rami fused, short ramus about 0.8 of CL, with 10 stout segments, lower ramus long, filiform; lower flagellum long, filiform.

Antenna (Fig. 1B) with basicerite bearing small acute lateral tooth; carpocerite about 0.3 of scaphocerite length, subcylindrical, moderately compressed, merocerite short, ischiocerite with acute medial process; flagellum long, filiform; scaphocerite about 4 times longer than wide, maximal width at 0.33 of length, lateral margin straight with well developed distolateral tooth, not exceeding distal border of broadly rounded lamella.

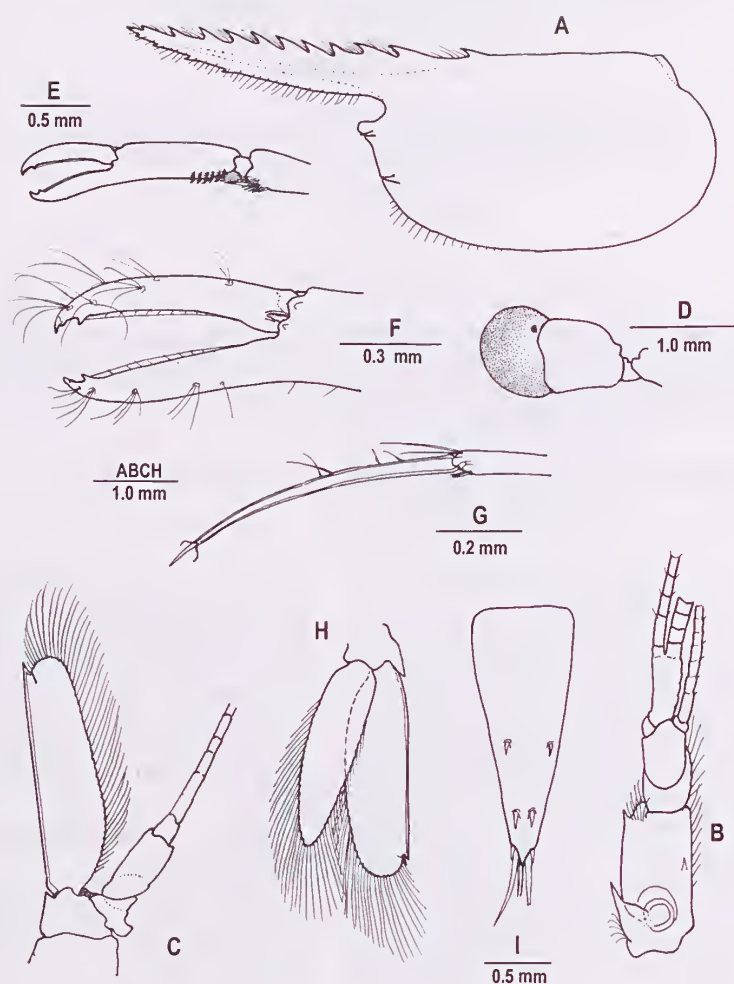


Fig. 1. *Leandrites stenopus* Holthuis. Male, Lucinda, Queensland, NTM Cr.012794. A, carapace and rostrum. B, antennule. C, antenna. D, eye. E, first pereiopod, chela. F, same, fingers. G, third pereiopod, dactyl and distal propod. H, telson. I, uropod.

Abdomen with sixth segment about 0.45 of CL, 1.3 times longer than deep; 2.3 times longer than fifth segment, posterolateral angle well developed, acute, posteroventral angle rounded, with small acute preterminal tooth, fourth pleuron posteroventrally rounded, fifth pleuron small, posteroventrally acute.

Telson (Fig. 1I) about 0.6 times sixth abdominal segment length, 2.5 times longer than anterior width, lateral margins straight, posteriorly convergent, dorsal spines small, at about 0.5 and 0.8 of telson length, anterior pair smaller, about 0.75, and further apart than posterior pair, posterior width about 0.25 of anterior width, acutely pointed (Fig. 3J), lateral spines small,

about size of anterior dorsal spines, marginal, medial spines well developed, stout, about 0.3 of telson length, subventral, submedian setae half length of medial spines, slender, sparsely setulose, subventral.

Mandible (Fig. 2A) robust, without palp, with stout four-toothed molar process, incisor process with three large acute teeth distally. Maxillula (Fig. 2B) with distinctly bilobed palp (Fig. 3C), lower lobe with small distal tubercle bearing short hooked seta; upper lacinia with about 12 stout simple spines distally; lower lacinia with numerous shorter spiniform setae distally. Maxilla (Fig. 2C) with basal endite bilobed, lobes slender, subequal, with sparse slender setae distally, palp tapering

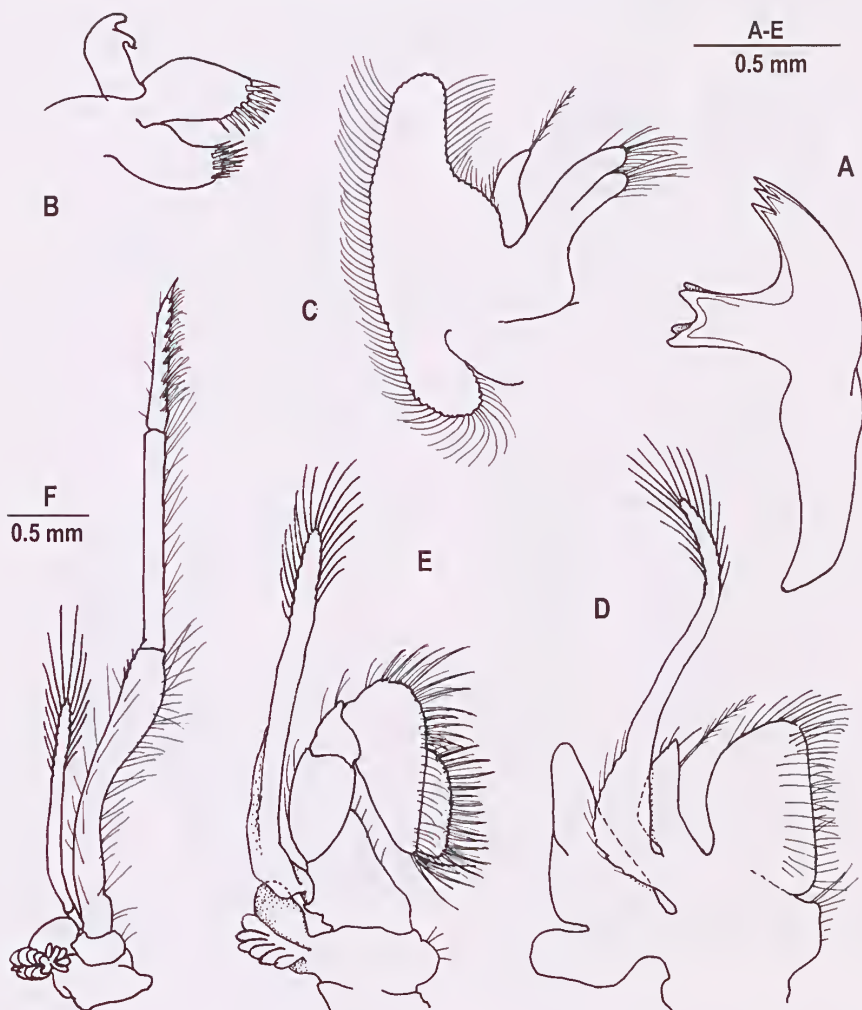


Fig. 2. *Leandrites stenopus* Holthuis. Male, Lucinda, Queensland, NTM Cr.012794. A, mandible. B, maxillula. C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped.

distally with single terminal plumose seta, proximal lateral border with short plumose setae, seaphognathite 2.7 times longer than wide, broad centrally, narrow anteriorly, with small posterior lobe. First maxilliped (Fig. 2D) with basal endite large, broad, distally rounded, distal and medial borders with numerous fine, mainly simple setae, coxal endite distinct, distomedially angular, sparsely setose, palp tapering, distally angular, with long preterminal plumose seta medially, short simple setae distally, exopod well developed, with numerous plumose setae distally, caridean lobe small, narrow, sparsely setose, epipod large, deeply bilobed distal lobe much larger, triangular, proximal lobe smaller rounded. Second

maxilliped (Fig. 2E) with dactylar segment short, broad, about 3.0 times longer than width, 0.6 of propodal segment length, with numerous long serrulate spines along medial margin, propodal segment broadly expanded distomedially, rounded, with numerous long serrulate spines medially, carpus and ischiomerus normal, exopod well developed, with numerous plumose setae distally, ramus expanded proximolaterally, basis medially produced, rounded, with small sub-oval epipod laterally, with small multi-lamellar podobranch. Third maxilliped (Fig. 2F) slender, ischiomerus completely fused with basis, junction indicated by small medial notch, about 15 times longer than central width, distally

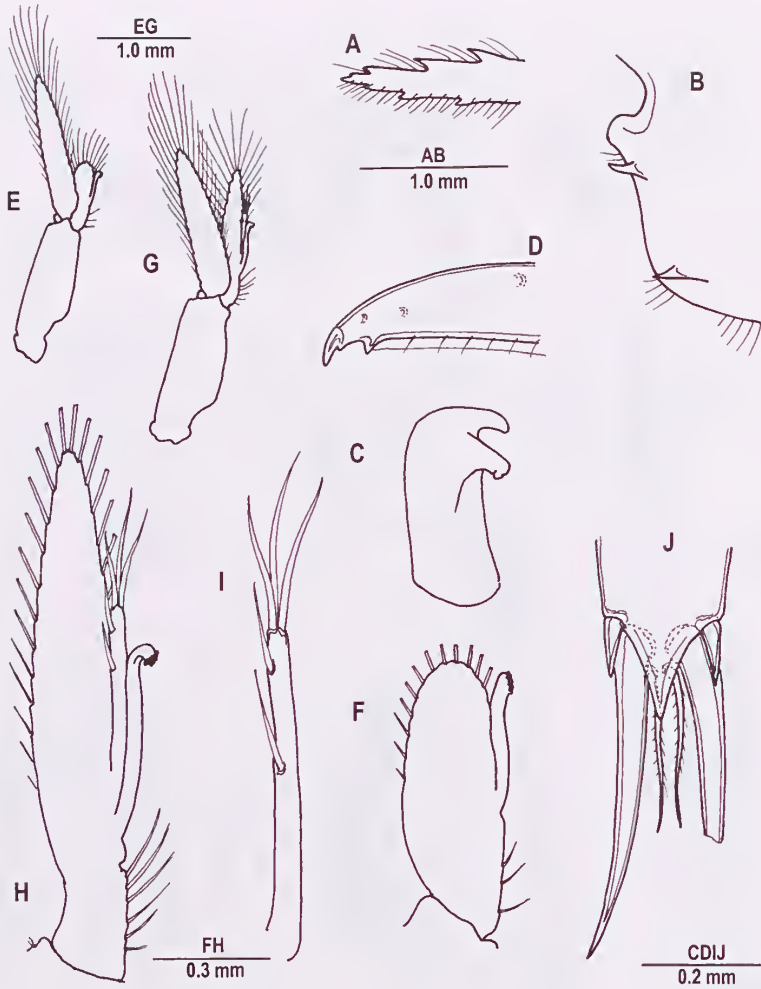


Fig. 3. *Leandrites stenopus* Holthuis. Male, Lucinda, Queensland, NTM. Cr.012794. A, tip of rostrum. B, inferior orbital angle. C, maxillula, palp. D, first pereiopod, distal dactylus. E, first pleopod. F, same, endopod. G, second pleopod. H, same, endopod. I, same, appendix masculina. J, telson, posterior spines.

broadened to about double central width, with three small spinules distolaterally, medial margin sparsely setose, carpal segment subcylindrical, about 12 times longer than wide, sparsely setose medially, distal segment about 0.6 of carpal segment length, with strong distal spine, medially with nine transverse rows of spiniform setae; endopod well developed, reaching to about 0.75 of ischiomeral segment length, with numerous plumose setae distally; coxa medially produced, sparsely setose, lateral plate well developed, rounded, with small lamellar arthrobranch proximally.

Pleurobranchs 5.

Fourth thoracic sternite with small acute medial process.

First pereiopod as previously described. Slender, with chela (Fig. 1E) about 0.75 of propod length, 0.68 of meral length; chela with palm slightly compressed, about 3.5 times longer than depth, with six transverse rows of short serrate setae proximally, fingers (Fig. 1F) sparsely setose, about 0.8 of palm length, similar, stout, feebly hollowed medially, about 5.5 times longer than proximal depth, with acute hooked tips, with small acute tooth (Fig. 3D) proximally, rest of cutting edge laminar, entire.

Third pereiopod slender, dactyl (Fig. 1G) about 0.33 of propod length, slightly curved, about 17 times longer than proximal depth, unguis feebly demarcated, about 0.12 of corpus length, with two slender setae at half dorsal margin length, smaller setae proximally, two

sensory setae distolaterally, propod subequal to CL, with two small distoventral spinules, six smaller ventral spinules. Fourth and fifth pereopods generally similar.

First pleopod (Fig. 3E) with endopod (Fig. 3F) about half exopod length, sub-oval, about 2.75 times longer than central width, distal and lateral borders with short plumose setae, proximal medial border with three spiniform setae, with well developed appendix interna arising at 0.5 of medial margin, not exceeding distal border of ramus. Second pleopod (Fig. 3G) with endopod (Fig. 3H) about 0.95 of exopod length, with numerous long plumose marginal setae, appendices arising at about 0.3 of medial margin length, appendix masculina (Fig. 3I) about 0.3 of endopod length, slender, subcylindrical, 12 times longer than proximal width with three slender serrulate terminal spines, about half appendix length, 2 shorter simple distolateral spines.

Uropod (Fig. 1H) with rami distinctly exceeding telson, protopodite posteriorly acute; exopod 3.4 times longer than central width, lateral margin straight with small distal tooth, with mobile spine medially, diaeresis obsolete, distal lamella reduced.

Measurements. CL approx. 3.4 mm.

Colouration. Unknown.

Habitat. Water temperature 25.4°C; salinity 34.9 ppt; sea floor firm, featureless sand/mud, 5.6 km offshore.

Remarks. The specimen generally agrees closely with the original description. The type specimen has only three ventral rostral teeth, in contrast with four in the present specimen. The rostral dentition can therefore be 1 + 10/3-4. Not reported in the original description are the small preterminal accessory teeth on each of the fingers of the first pereopods. No similar teeth have been reported in other palaemonid genera.

Discussion. The original specimen was collected on March 8, 1899 and no further specimens have been subsequently described during the following century. The discovery of a second specimen, albeit damaged and incomplete, shows that the species is still extant and of wider distribution. The assessment of rarity in marine habitats remains an unsolved problem. A terrestrial species that has not been observed over a period of 50 years is deemed extinct (Baillie and Groombridge 1996). Li and Manning (1998) reported the presence of this species in the northern South China Sea but provided no further details.

The slender build and appendages of this shrimp suggests that it is a free-living soft bottom species. The holotype was collected from 56 m on a radiolarian ooze substrate.

Chace and Bruce (1993) commented that the generic position of this species could not be fully ascertained until a male had been collected, enabling the condition of the first pleopod to be determined. This has now been rectified and the presence of an appendix interna on the

first pleopod endopod confirms that this species belongs in the genus *Leandrites*. The presence of a median sternal tooth on the fourth thoracic sternite is noted; a similar tooth is also present in *Leandrites celebensis* (De Man, 1881), a feature that is probably another character of generic value (Bruce 1987). It is found in some genera in both the Palaemoninae and the Pontoniinae and its phylogenetic importance is yet to be evaluated.

The fingers of the second pereopod chela in *Leandrites stenopus* appear to be unique amongst the Palaemoninae, with the small acute preterminal teeth. It remains possible that these may have been overlooked in other species as, although distinctive, they are very small and not readily discernible when the fingers are closed.

Four species of the genus *Leandrites* are now known, all from the central Indo-West Pacific region, and a key for their identification is provided by Chace and Bruce (1993). The commonest and most widely distributed is *L. celebensis*, recorded from southern India, Indonesia and tropical Australian waters, from shallow brackish waters. The three other species are all south east Asian. *Leandrites indicus* Holthuis, 1950, is known from the type specimen from Sulawesi, Indonesia, and Vietnam (Nguyen Van Xuan 1992), where it is common in mangrove creeks and rivers; *L. deschampsii* (Nobili, 1903), from three specimens from the type locality, Singapore, and one further specimen from China (Liu *et al.* 1990); *L. stenopus* is now definitely known from two specimens only, from off Java, Indonesia, and north east Queensland, Australia, and probably also the northern South China Sea.

The present record also contrasts with the original discovery and indicates that the species may also occur in shallower water (15 m *versus* 56 m) and on non-radiolarian substrates.

ACKNOWLEDGMENTS

I am most grateful to Dr Frank Hoedt for the opportunity to examine the specimen on which this report is based, and Dr C.H.J.M Fransen, for drawing my attention to the abstract by Li and Manning. This study was carried out with the support of the Australian Biological Resources Study.

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Onycocaridella prima Bruce, 1981, a rare pontoniine shrimp from Darwin Harbour (Crustacea: Decapoda: Pontoniinae)

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ABSTRACT

The second occurrence of the pontoniine shrimp *Onycocaridella prima* Bruce, 1981 is recorded. The single specimen was found in a sponge host collected from Darwin Harbour, Northern Territory, Australia. The species is otherwise known only from the type specimens from Heron Island, Queensland.

KEYWORDS. *Onycocaridella prima*, Crustacea, Pontoniinae, Darwin Harbour, sponge associate, Australia.

INTRODUCTION

In the course of a survey of the marine fauna of the Port of Darwin, carried out by marine scientists from CSIRO Centre for Research on Introduced Marine Pests (CRIMP) and staff of the Museums and Art Galleries of the Northern Territory in 1998, a single specimen of a small pontoniine shrimp was obtained from a sponge host collected from harbour piles. The specimen was identified as *Onycocaridella prima*, a species previously known only from the two type specimens collected in 1979 from Heron Island in the Capricorn Islands of the Great Barrier Reef. The new specimen of this apparently rare shrimp is here described and compared with the type material from Queensland.

Abbreviations used: CL, post orbital carapace length; NTM, Museum and Art Gallery of the Northern Territory.

SYSTEMATICS

Onycocaridella prima Bruce, 1981

(Fig. 1)

Onycocaridella prima Bruce, 1981a: 243-250, figs. 1-6.

Material examined. 1 ovig. ♀, stn NTD FHI PI-3, Fort Hill Wharf, Port of Darwin Harbour, 12°28.322'S 130°50.826'E, depth 3-9 m, collected by hand from pile scrapings, 15 August 1998, coll. CSIRO CRIMP team, NTM Cr012795.

Description. A stout shrimp, with body sub-cylindrical, slightly compressed anteriorly, with relatively large abdomen. Generally as in original description.

Rostrum about 0.22 of CL, acute, slender, depressed, slightly up-turned, unarmed. Carapace (Fig. 1A) about as long as maximal depth, smooth, devoid of spines and teeth. Abdomen slightly compressed, with first three pleura broadly expanded.

Chelae of second pereiopods similar, only slightly unequal; major chela (Fig. 1B) with fingers 0.47 of palm length; minor chela (Fig. 1C) fingers 0.57 of palm length, dactyls with sinuous entire cutting edges.

Third pereiopods with propod stout, bearing two short stout distoventral spines; dactyl (Fig. 1D) with distinctly demarcated unguis, corpus with ventral cutting edge straight, without distal accessory tooth, with several small denticles proximally.

Ova numerous, small.

Measurements. CL 3.3 mm; length of ovum 0.8 mm.

Host. *Mycale* sp., [Porifera: Mycalidae], possibly *Mycale* (*Aegagropila*) cf. *obscura* (Carter).

Distribution. Previously reported only from the type locality, Heron Island, Capricorn Islands, Queensland, on the southern Great Barrier Reef, at 12 m depth.

Remarks. The single specimen is complete and in good condition and in general agrees well with the original description. With a CL of 3.3 mm, it is considerably larger than both the type specimens (♂ allotype 1.8 mm; ♀ holotype 1.75 mm) suggesting that both of these were juvenile specimens. With ova, the present specimen is clearly an adult. In the adult, the carapace length is less than the carapace depth, whereas in the juvenile types it is greater (Fig. 1E), the rostrum is also more depressed, without a small preterminal dorsal tooth as in the holotype. In the holotype female the second pereiopod chelae are markedly unequal in size (2.0:1.0), in the present specimen they are only slightly unequal (1.09:1.0), with the major chela

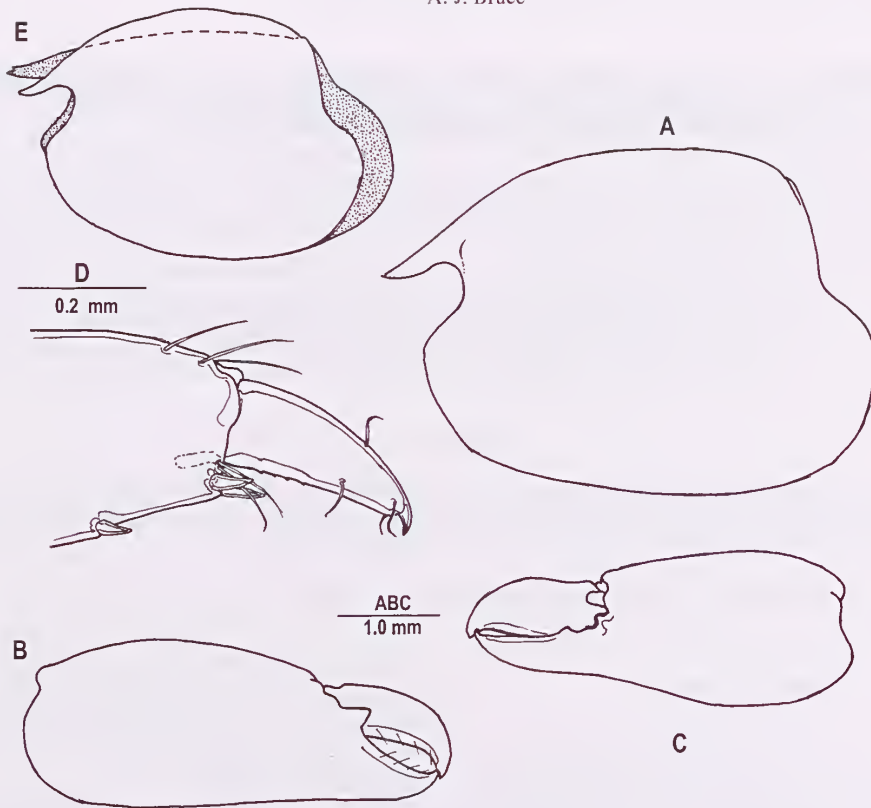


Fig. 1. *Onyccaridella prima* Bruce, ovigerous female, Darwin Harbour, NTM Cr012795. A, carapace, lateral. B, second pereopod, major chela. C, same, minor chela. D, third pereopod, distal propod and dactyl. E, comparison of carapace shapes in adult and juvenile (stippled) specimens to show relative profiles (not to scale).

relatively smaller, 1.29 times the CL, as opposed to 2.0 times the CL in the holotype. The ambulatory dactyl of the third pereopod is essentially as in the holotype but lacks the small distoventral accessory tooth and the distal ventral margin of the corpus appears unarmed. The absence of these small denticles may be merely the result of abrasion. The proximal ventral margin bears about six minute denticles.

The host sponge has not been identified with full certainty. The preserved sample contained representatives of several sponge genera (J.N.A. Hooper, personal communication), but these included material referable to a *Mycale*, possibly *Mycale* (*Aegagropila*) cf. *obscura* (Carter). As the type specimens of *O. prima* were found in association with *Mycale sulcata* Hentschel, it is most probable that this further *Mycale* was the host of the present specimens.

The key to the genus *Onyccaridella* Bruce, accompanying the original description of *O. prima* remains valid (Bruce 1981a). The two other species of the genus, *O. stenolepis* (Holthuis, 1952) and *O. monodoa* (Fujino and Miyake, 1969) have also both been recorded in Australian waters, also from Heron Island (Bruce 1981b, 1983).

ACKNOWLEDGMENTS

I am most grateful to Helen Barnes for the opportunity to examine the specimen on which this report is based and to Dr J.N.A. Hooper for the identification of the sponge host. This study was carried out with the support of the Australian Biological Resources Survey.

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Biological observations on the commensal shrimp *Paranchistus armatus* (H. Milne Edwards) (Crustacea: Decapoda: Pontoniinae)

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ABSTRACT

Some aspects of the biology of the commensal pontoniine shrimp, *Paranchistus armatus* (H. Milne Edwards), on the Great Barrier Reef, are reported. The species is an obligatory commensal living as heterosexual pairs only in the giant clam, *Tridacna gigas* (L.). Features of the morphology, fecundity, population structure, infection rate, and reproductive mechanisms are described. It is considered possible that the species shows indications of serial male protandrous hermaphroditism, not previously noted to occur in shrimps of the subfamily Pontoniinae. It may also be considered an endangered species as its host animal is under threat.

KEYWORDS: *Paranchistus armatus*, Pontoniinae, Decapoda, biology, possible hermaphroditism, *Tridacna gigas* commensal, Australia, Great Barrier Reef, endangered species.

INTRODUCTION

The pontoniine shrimps associated with bivalve hosts have attracted a certain amount of biological study, particularly the species of the genera *Anchistus*, *Paranchistus* and *Conchodytes*, found in association with hosts in the family Pinnidae (Johnson and Liang, 1966; Hipeau-Jacquotte 1974; Morton 1987). The species associated with the family Tridacnidae have received little attention, probably as the result of the clam's legal protection on most coral reefs and a reluctance to sacrifice a significant number of these hosts.

The shrimp *Paranchistus armatus* is unusual in the subfamily Pontoniinae, as it is one of the largest species known, and is found only in association with the giant clam *Tridacna gigas* (L.). The latter has a restricted distribution in the Malaysian-Western Pacific region (Rosewater 1965) and the shrimp, although first described by Henri Milne Edwards in 1837, has so far only been recorded from a relatively small number of localities within that region. The giant clam is now a protected species in Queensland waters, where specimens can only be collected by special permit. The Queensland Fisheries Service has been carrying out an investigation of the biology of *T. gigas*, which has enabled numerous specimens of *P. armatus* to be examined without involving any unnecessary sampling of the host animal. Previous reports on these shrimps have generally been concerned with one to three individuals and the present collection of 164 specimens

represents the first time that a small population, together with some data concerning the hosts, have been available for study. I am most grateful to Dr R.G. Pearson, of the Queensland Fisheries Service, Department of Primary Industry, and Dr V. Harriot, for this opportunity to report upon these specimens.

Measurements (mm) refer to the postorbital carapace length (CL) of the shrimps. Representative specimens have been deposited in the collections of the Northern Territory Museum, Darwin, (Cr.008674) and the Queensland Museum, Brisbane (W25447).

DESCRIPTION

Paranchistus armatus (H. Milne Edwards, 1837) (Figs 1-3)

Restricted synonymy:

Pontonia armata H. Milne Edwards, 1837: 359.

Anchistus binnguiculatus Borradaile, 1898: 387.

Tridacnocris binnguiculatus - Nobili 1899: 235.

Anchistus oshimai Kubo, 1949: 26

Paranchistus binnguiculatus - Holthuis 1952: 13, 93-97, figs 36-38.

Anchistus armatus - Bruce 1967: 564-568.

Paranchistus armatus - Bruce 1975: 49-54, figs 1-3.

Material examined. (i) 61 adult pairs, 5 ovig. ♀, 2 ♀, 4 ♂, 3 immature, Arlington Reef, 16° 45.0'S, 146° 00.0'E, from reef flat, 2 November 1978 to 12 November 1979. (ii) 4 pairs, 15 juveniles, Hastings Reef, 26 November 1979. (iii) 1 pair, 1 ♂, 3 juveniles, Michaelmas Cay, 5 December 1979.

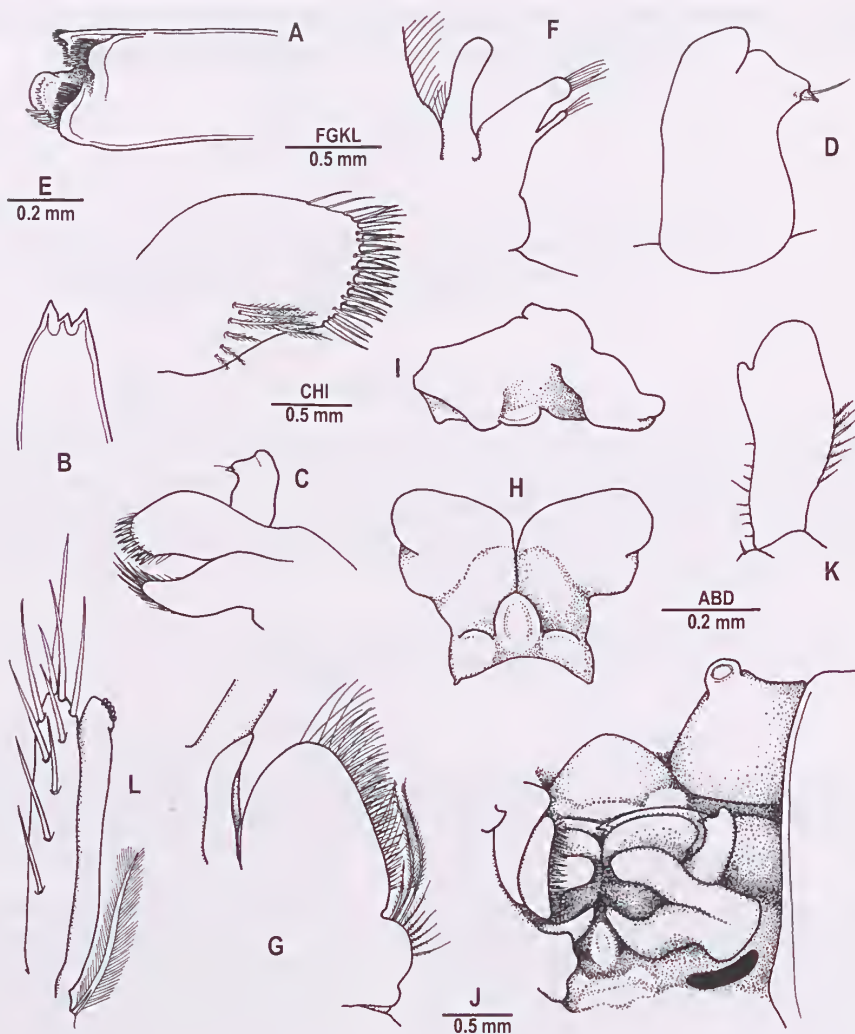


Fig. 1. *Paranchistus armatus* (H. Milne Edwards), Arlington Reef, Queensland, Australia. A, left mandible. B, same, incisor process. C, maxillula. D, same, palp. E, same, upper lacinia. F, maxilla. G, first maxilliped, palp and endites. H, paragnaths, ventral aspect. I, same, left lateral. J, buccal region, left maxilla to third maxilliped removed. K, first pleopod, endopod. L, second pleopod, endopod, appendices. A-J, ovigerous female. KL., male.

Morphology. The present specimens agree closely with the previously published descriptions given by Kubo (1949, as *Anchistus oshimai*), Holthuis (1952, as *P. biunguiculatus*), and Bruce (1975).

In the large specimens, particularly the females, the hepatic spine is very small and could only be identified with considerable difficulty, even in dry specimens. The dorsal rostral dentition on small specimens is relatively conspicuous, in contrast to the condition in large females in which it is obsolete.

The mouthparts correspond closely with the illustrations provided by Holthuis (1952). The maxillula has short simple spines along the inner aspect and simple

setae on the outer side of the distal margin of the upper lacinia (Figs 1 C, E). The palp is bilobed, with a short simple seta on the lower lobe (Fig. 1 D). The maxilla has the basal endite bilobed, with the distal lobe larger than the proximal and bearing six short setae, in contrast to five (Fig. 1 F). The palp is broad and flattened, without a subterminal seta but with a few short plumose setae on the proximal lateral border. The setae on the endites of the first maxilliped are simple. The coxal endite bears a single long slender seta. The palp is non-setose and the caridcan lobe of the exopod is fringed with short plumose setae. The dactyl of the second maxilliped is provided with numerous finely serrated spiniform setae

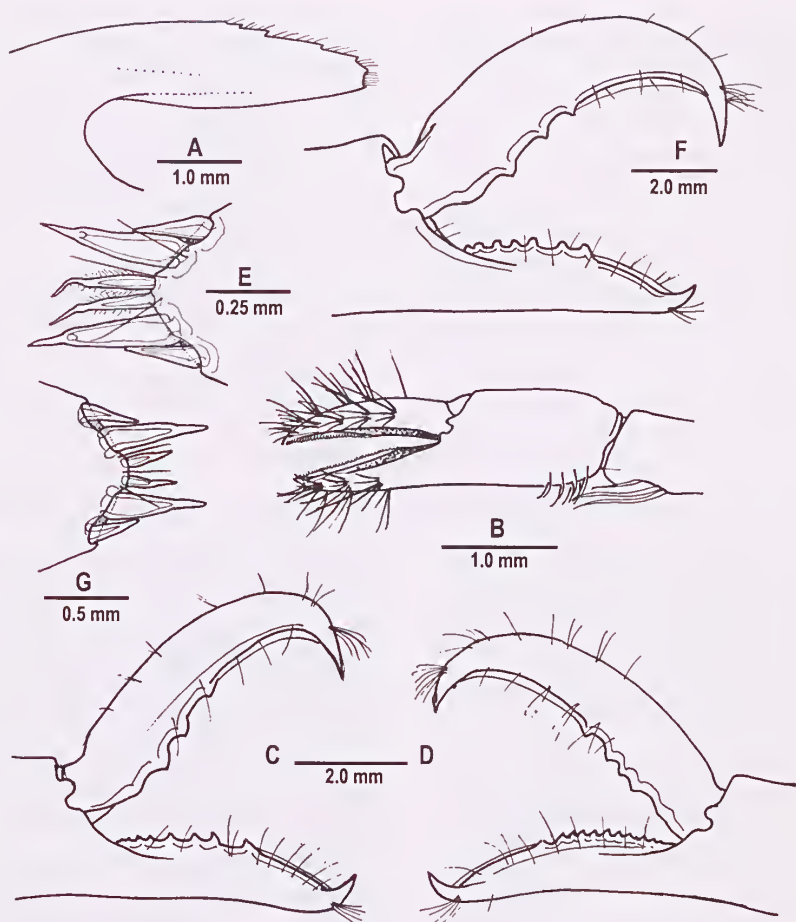


Fig. 2. *Paranchistus armatus* (H. Milne Edwards), Arlington Reef, Queensland, Australia. Male, CL 8.0 mm. A, rostrum. B, chela of first pereiopod. C, fingers of right second pereiopod. D, fingers of left second pereiopod. E, posterior telson spines. Female, CL 14.0 mm. F, fingers of second pereiopod. G, posterior telson spines.

(Fig. 1 J). The anteromedial border of the propodal segment bears long slender simple spines. The setae of the third maxilliped are simple (Fig. 1 G). The epipods of the three maxillipeds are deeply bilobed, subrectangular and oval respectively (Figs 1 K, L). The third maxilliped also bears a small six lamellar arthrobranch. The flagella of all exopods are well developed and broad, with numerous plumose setae along the margins of the distal third.

The chelae of the first pereiopod are subspatulate, with the laterally situated cutting edges of the fingers fully finely pectinate (Fig. 2 B). The fourth thoracic sternite bears a low transverse ridge with a small median notch, and a similar but slightly large ridge is also present on the fifth sternite.

The second pereiopods are generally subequal and similar in both males and females, but relatively larger in the former (Figs 2 C, D, F). The dactyl is generally armed with 3-4 small acute teeth on the proximal cutting

edge and the fixed finger has 7-12, the most proximal of which may be very small.

The telson is provided with three pairs of posterior spines and two pairs of small dorsal spines (Figs 2 E, G). The latter are situated at about 0.70 and 0.85 of the telson length. The dorsal spines are relatively longer in the males. The intermediate posterior spines are about 4.5 times longer than wide, about 0.1 of the telson length, and about twice the length of the lateral spines. The submedian spines are slender, feebly setulose and 0.4 - 0.7 of the length of the intermediate spines.

Colouration. The body, antennal peduncles, second pereiopods and caudal fan are white, with the antennal flagella purplish.

BIOLOGY

Fecundity. Of the 73 females over 11 mm CL, all except four were ovigerous, and one of these appeared

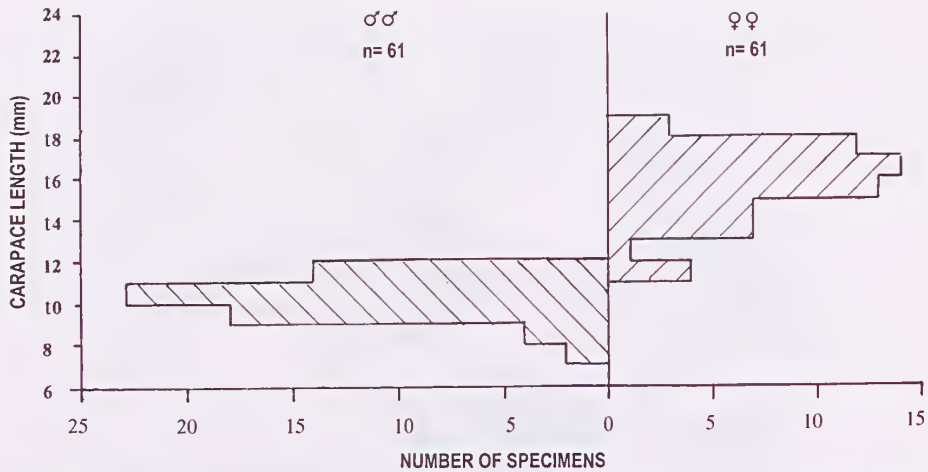


Fig. 3. *Paranchistus armatus* (H. Milne Edwards), carapace length distributions of the paired specimens from Arlington Reef.

to have just hatched its ova. The smallest ovigerous female, CL 11 mm, carried 1,550 ova, and the largest, CL 18 mm, carried 8,901 ova. Intermediate size females carried the following numbers of ova: (i) CL 13 mm, 4646; (ii) CL 15 mm, 5638; (iii) CL 17 mm, 7,788. The ova are about 0.5 mm in length when freshly laid and 1.7 mm when about to hatch.

Population structure. Of the 138 specimens from Arlington Reef, the males ranged in size from CL 7-11 mm and the females 8-18 mm. No juveniles below CL 7 mm were found and the appendix masculina is recognisable in males of this carapace length. The distribution of carapace length is shown in Figure 3.

It is noteworthy that no males occur with a CL of over 12 mm and that very few females occur with a carapace length below 11 mm, less than 3 %. As males are readily identifiable from CL, 7-11 mm, it appears that this population did not contain any juvenile females and suggests that males of this species may be a protandrous hermaphrodites, with the transition from male to female occurring at about CL 11 mm.

In general the larger females are paired with the larger males but considerable variation exists and a larger sample is needed to clarify apparent discrepancies. The relationships are summarised in Table 1.

Table 1. Range of carapace length (CL) in males paired with females of specified CL.

♀ CL	♂ CL, range	n	mean
11	8 - 11	5	9.8
12	7 - 9	2	8.0
13	9 - 11	6	9.6
14	7 - 10	7	8.2
15	9 - 11	15	10.5
16	8 - 11	14	9.7
17	9 - 11	13	10.4
18	10 - 11	3	10.6

Almost all specimens were found as male-female pairs. At Arlington Reef, 61 pairs were collected, together with 6 six ovigerous females without male partners and 2 non-ovigerous females, CL 16 and 8 mm. It is most probable that the males of the six ovigerous females were overlooked in dissection of the host clam, or escaped during its removal from the reef. Of the four cases where isolated females were found, three were small, CL 8 mm, and could have been without males or again, the males may have been overlooked during collection.

In only one instance, at Arlington Reef, was more than a pair of shrimps found in the host clam. In this case a pair of small individuals, both of CL 10 mm were accompanied by an additional small male of 7.5 mm CL, the smallest identifiable male found. The female of this association was without ova.

The two largest female shrimps (both 18 mm CL) were found in two of the largest host clams, with shell lengths of 83 cm and 95.5 cm. Two larger clams from Hastings Reef were sampled, valve length 100 cm and 102.5 cm, both with a breeding pair of shrimps. The smallest breeding pairs of shrimps were of 7.5 and 12 mm CL, and 10 and 11.5 mm CL in clams of 37.1 cm and 43.0 cm respectively. The smallest pair of shrimps, CLs 4.5 and 5.0 mm, were from Hastings Reef, from a clam of 22.2 cm valve length.

Juveniles. The Arlington Reef population of *P. armatus* is remarkable for the apparent absence of juveniles, although sampling was carried out in the months November, December, January, July, August, September and October and ovigerous females were found at all times, so that breeding may occur throughout the year. Additional samples were also collected from Hastings Reef, where clams of a larger size and smaller size were sampled. At Hastings Reef two juveniles CL 4.5 and 5.0 mm, were found in clams of valve lengths

28 and 23 cm respectively. A pair with an ovigerous female were also found in a clam of valve length 43 cm. At Michaelmas Cay, eight additional small specimens of *T. gigas* were sampled, of which three contained juveniles shrimps CL 4, 4, and 5 mm, clam valve lengths 30, 31 and 27 cm respectively. One clam, valve length 34 cm, contained a single male, CL 7 mm, and another, valve length 37 cm., a small pair with an ovigerous female, CLs 7.5 and 12 mm.

Two particularly large clams were also examined at Hastings Reef in November 1979, valve lengths 100 and 102 cm. Each contained a male-female pair of adult shrimp, CLs 11 and 15 mm and 11 and 17 mm. These were accompanied by 7 and 6 juvenile shrimp respectively, CLs 1.5, 4, 4, 4, 5.5, 7, 7 mm and 4, 4.5, 5, 6, 7, 7 mm in each case. The 1.5 mm CL specimen was the smallest found and is probably only a little over the first post-larval stage size.

Autotomy. 89 specimens were examined in detail for evidence for autotomy and limb regeneration. In not a single example was there any evidence of limb loss, injury or regeneration.

Host. All specimens were found in association with the giant clam *Tridacna gigas* (L.). Hosts sampled ranged in size from 22 - 102 cm in valve length. Small numbers of *Tridacna crocea*, *T. derasa*, *T. maxima*, *T. squamosa* and *Hippopus hippopus* were also sampled from Michaelmas Cay but all were without associated *P. armatus* (Pearson pers. comm.). The exact situation within the host clam was not observable or recorded.

Infestation rate. Details are available of 91 clams from Arlington Reef. Of these, 84 contained associated shrimps, giving an infection rate of 92.3 %. Including clams from other localities, 118 clams were infested on 100 occasions, with an overall infection rate of 84.7%.

Associated fauna. One specimen of *Tridacna gigas*, valve length 18.2 cm, also contained two specimens of the pinnotherid crab *Xanthasia murigera* White in addition to *Paranchistus armatus*. No bopyrid parasitization of the shrimps was found.

Distribution. *Type locality:* New Ireland, Papua New Guinea. Also known from *Indonesia:* Batanta; Mefour (Nobili 1899); Obi Latu (Holthuis 1952); *Papua New Guinea:* New Ireland (H. Milne Edwards 1837); Tubetube, Engineer Islands (Borradaile 1898); Hansa Bay (De Grave 1999); *Australia:* Undine Reef (McNeill 1968); Chapman Island (Bruce 1975); Cairns; Arlington Reef, Michaelmas Cay (Bruce 1983); *Caroline Islands:* Helen Atoll, Palau (Kubo 1949); Ngadarak Reef and Ngaianges Island (Miyake and Fujino 1968); *Marshall Islands:* Ujae Atoll (Holthuis 1953); Eniwetak Atoll (Rosewater 1965; Bruce 1975; Bruce 1979; Devaney and Bruce 1989); Bikini Atoll (Chace and Bruce 1993); *Kiribati:* Onotoa Atoll (Holthuis 1953).

Remarks. Giant clams are notorious for their longevity and it may be safely assumed that each clam

provides a home for many generations of commensal shrimp. No information is available on the life span of the infesting shrimps. Their relatively large size, in relation to other pontonine shrimps, may indicate that they live longer than about 12 months as suggested for *Periclimenes ornatus*, a small pontonine associate of Japanese sea anemones (Omori *et al.* 1994). Morton (1987) has discussed the biology of the commensal pontonine shrimps, *Auchistus custos* (Forsskal) and *Conchodytes monodactylus* Holthuis, 1952, associated with the pinnid bivalve *Pinna bicolor* Gmelin. This host is comparatively short lived in comparison with *T. gigas* and the situation is not comparable. No information is available on the recruitment of these shrimps but it seems likely that they arrive as post-larvae from the plankton. In the present study the smallest individuals were little above the typical size of pontonine post-larvae. The small ova indicate that there is no abbreviated larval development that would enable recruitment to be derived from the occupying pair of shrimps. The frequency of heterosexual pairs of adult shrimps only also suggests that, in general, their presence suppresses or prevents further colonisation by juveniles. The high infestation rate suggests that replacement of shrimps is efficient and quick. The range of shrimps sizes indicates a continuous process without marked seasonality. Possibly the death of an adult female results in the change of the male partner into a female and the recruitment of a new shrimp from the larvae in the plankton, which would develop into a male. Death of a male would follow similar recruitment, with the post-larva also developing into a male. Protandrous and simultaneous hermaphroditism have been reported in a number of caridean shrimp families (Bauer and Holt 1998) but sex changes have so far not been recorded in the Palaeomonidae.

The absence of any signs of trauma or autotomy suggests that life in *Tridacna gigas* represents a particularly secure niche. This may be contrasted with the situation reported in *Coralliocaris graminea* (Dana) living in *Acropora* corals (Bruce 1976), where signs of damage to the shrimp were frequent. In this species a minimum of 23% of specimens examined showed signs of significant regeneration after serious damage. The species lives in small communities depending upon the size of the coral host. The incidence of damage increases with the size of the population, reaching up to 77% in the larger populations. This damage was attributed to intraspecific combat, particularly between females (Bruce 1976), factors that would not be present in the case of *P. armatus*.

The giant clam, *Tridacna gigas* (L.), was formerly widely distributed in the Malaysian — northern Australian — Western Pacific- region (Rosewater 1965) but has recently been reported as “? extinct” in Taiwan, Vanuatu, Fiji, Guam, New Caledonia and the Northern Marianas (Wells 1997). Although unreported from these

localities, it is likely that *P. armatus* was also present in these regions but is now similarly extinct. All species of Tridacnidae are listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora, APPENDICES I and II, as adopted by the Conference of the Parties, valid from 16 February 1995 (<http://www.iwec.org/cites1.htm>). If *T. gigas* is considered to be an endangered species, logically its obligate “commensal” associate, *P. armatus*, must be in equal danger.

Much remains to be studied in the life histories of “commensal” shrimps such as *Paranchistus armatus* and most others. Information on their food and feeding habits is minimal, as is data on their larval stages and life history, mechanism of host colonisation, longevity and reproductive biology. The term “commensalism” is frequently a euphemism for ignorance of details of the lifestyle involved.

ACKNOWLEDGMENTS

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Vibration signals in Australian fiddler crabs - a first inventory

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ABSTRACT

Vibration signals (often called sounds), which are components of the subterranean communication system of fiddler crabs, were recorded in 14 of the 17 confirmed *Uca* species of Australia and analysed by use of oscillograms. Signals of the related crab *Heloeccius cordiformis* and two Asian species of *Uca* were used for comparisons. All crabs studied produce "bounces", i.e. burst-pulsed sounds corresponding to laterally directed jerks of the whole animal. All species except *H. cordiformis*, *U. dampieri* and *U. vomeris* also emit "drumwhirls" or "rolls", the familiar rapping sounds of the major cheliped. Parameters of these drumwhirls were compared using aquarium sound recordings of males competing for a burrow. Indications of character displacement were found with regard to western and eastern samples of *U. signata*. The most advanced rapping signals were recorded in *U. signata* and *U. flammula* and in the two Asian species, *U. rosea* and *U. annulipes*; the most simple ones were recorded in *U. longidigitum* and *U. polita*. The two latter appear to have preserved early stages of drumwhirl evolution, contributing to the assumption of an Australian origin of the genus *Uca*.

KEYWORDS. Crustacea, Brachyura, Ocypodidae, *Uca* and *Heloeccius*, vibration signals, survey, early stages of evolution, Australian origin of *Uca*.

INTRODUCTION

Crabs inhabiting the semiterrestrial environment—mainly Sesarminae (Grapsidae) and the subfamilies of the Ocypodidae—are well-known examples of communication by vibration signals. Various types of such signals have been reported in literature (see preliminary synopsis in von Hagen 1975), the most important ones being generated by percussion and stridulation. Most research on signal production, transmission and reception has been done in fiddler crabs (*Uca*) and ghost crabs (*Ocypode*) (see Salmon 1983 for a review).

It is not clear to date, how often vibration signalling arose independently in the two crab families mentioned. It is certain, however, that vibration signals are used in both agonistic and courtship situations and occur mostly underground or at least in or near the mouth of the crab's burrow. Being short-range signals, vibrations appear to play a major role in reproductive isolation. At least in two West Indian sympatric and sibling species of *Uca*, vibration signals were found to be much more species-specific than the visual display (von Hagen 1984). As the signals can also have group-specific characters, they allow various phylogenetic inferences (von Hagen 1975, 1984), especially when these inferences are based on quantitative data.

Until now, quantitative studies of *Uca* bioacoustics have mainly dealt with the European fiddler crab *U. tangeri* (von Hagen 1962; Altevogt 1963, 1970) and American species of both the Atlantic (Salmon 1965, 1983; Salmon and Horsch 1972; von Hagen 1984) and Pacific coasts (Altevogt 1970; Müller 1989). R. Polivka (pers. com.) started a bioacoustic project on fiddler crabs of South East Asia, but did not complete and publish his studies. With respect to Australia, pertinent research seems to be lacking.

In the course of two visits to Australia, the author had the opportunity to record subterranean vibration signals of nearly all Australian species of *Uca* and of the related ocypodid *Heloeccius cordiformis*. The recordings were obtained using a special aquarium that allowed direct observation of the crabs during sound production (cf. von Hagen 1970, 1984). The oscillographic analyses published here are meant to serve as a first survey or inventory and thus as a basis for more specific research in future.

With a few exceptions, the vibration signals of Australian fiddlers are simple, especially when compared with the two Asian species included in this study. This result allows certain speculations: that some Australian *Uca* species have preserved an early stage of acoustic communication (early with respect to the whole genus) and that the genus probably originated in Australia.

Table 1. Abbreviations, systematic grouping, scientific names and Australian distribution of the species and origin of the samples studied. Roman group numerals of *Uca* as in George and Jones (1982); in parentheses: subgeneric names from Crane (1975), invalid except *Australuca*. Distribution in Australia: C circum-tropical, E eastern, W western.

Genus <i>Heloeccius</i> :			
Hc	<i>H. cordiformis</i> (H. Milne-Edwards)	E	Brisbane
Genus <i>Uca</i> , group IV (" <i>Thalassuca</i> "):			
dp	<i>U. dampieri</i> Crane	W	Darwin
vm	<i>U. vomeris</i> McNeill	E	Bamaga, Brisbane
Genus <i>Uca</i> , group III (<i>Australuca</i>):			
lg	<i>U. longidigitum</i> (Kingsley)	E	Brisbane
pl	<i>U. polita</i> Crane	C	Broome, Cairns, Darwin
hs	<i>U. hirsutimanus</i> George and Jones	W	Broome, Darwin
sg	<i>U. signata</i> (Hess)	C	Cairns, Darwin
el	<i>U. elegans</i> George and Jones	W	Darwin
ss	<i>U. seismella</i> Crane	C	Broome, Darwin
Genus <i>Uca</i> , groups I and II (" <i>Deltuca</i> "):			
cp	<i>U. capricornis</i> Crane	W	Bamaga, Darwin
ds	<i>U. dussumieri</i> (H. Milne-Edwards)	E	Bamaga, Cairns
fl	<i>U. flammula</i> Crane	W	Broome, Darwin
cc	<i>U. coarctata</i> (H. Milne-Edwards)	E	Brisbane
rs	<i>U. rosea</i> (Tweedie)	-	Penang and Malakka (Malaysia)
Genus <i>Uca</i> , group V (" <i>Celuca</i> "):			
mb	<i>U. njoebergi</i> Rathbun	W	Broome, Darwin
pp	<i>U. perplexa</i> (H. Milne-Edwards)	E	Bamaga, Cairns
an	<i>U. annulipes</i> (H. Milne-Edwards)	-	Bombay (India)

ANIMALS AND METHODS

Species names and localities of the specimens are given in Table 1. The endemic Australian oecypodid crab *Heloeccius cordiformis*, lately placed in a subfamily of its own (*Heloecciinae* Türkay 1983), was studied in the northern part of its range, which ends at Rockhampton (Davie pers. comm). The present knowledge of the geographic ranges of the Australian *Uca*, as specified in von Hagen and Jones (1989), is also briefly indicated in the Table.

Table 1 lists 14 of the 17 species of *Uca* confirmed for the Australian fauna (only *U. crassipes*, *U. tetragonon* and *U. triangularis* were not studied). As the discussion about the extent and proper naming of the species groups is not yet settled, Table 1 follows the grouping of George and Jones (1982) by Roman numerals; only *U. elegans* is transferred from group I to group III and the order of groups has been altered (see Discussion). In addition the subgeneric names from Crane's monograph (1975) are listed, which are widely in use though mostly (except *Australuca*) invalid because

of Bott (1973). The abbreviations of species names (Table 1) are used also in Figures 1 and 2.

The two Asian species, *U. rosea* and *U. annulipes*, included in the list, were collected by travelling students, and the sounds were recorded in Germany. The Australian species were studied at the places listed in Table 1 during July and August of the years 1986 and 1988. Outdoor recordings of subterranean signals of crabs are useful on certain occasions, but normally do not allow statements on how the sounds are generated (von Hagen 1975). Therefore, the signals were recorded indoors in aquaria (12 l, height 20.5 cm), which, using the technique of von Hagen (1970, 1984), allowed direct observation of subterranean activities of the crabs. Bricks were laid in the centre of the aquaria and only the narrow gap between these bricks and the plastic walls were filled with moist muddy sand from the habitat of the animals. The crabs were forced to dig their burrows within this thin vertical layer of soil and were observed, at very close quarters, through the wall, which had to be kept clean.

Though also called "sounds", the signals recorded act as substrate-borne vibrations; the air-borne

Table 2. Burst-pulsed sounds ("bounces") measured in males of *Heloeccius cordiformis* and four Australian *Uca* species (repetition rates calculated from means of preceding column).

Species	One bounce: seconds		Sequences: maximum number of bounces	One bounce plus subsequent silent interval: seconds		Repetition rate: bounces per second	Number of bounces measured (males)
	mean	s.d.		mean	s.d.		
<i>H. cordiformis</i>	0.30	± 0.10	3	0.64	± 0.24	1.56	22 (2)
<i>U. vomeris</i>	0.12	± 0.04	15	0.39	± 0.19	2.56	23 (2)
<i>U. seismella</i>	0.07	± 0.02	43	0.19	± 0.02	5.26	64 (5)
<i>U. coarctata</i>	0.25	± 0.08	4	0.57	± 0.13	1.75	21 (3)
<i>U. mjoebergi</i>	0.20	± 0.06	6	0.69	± 0.14	1.45	64 (5)

components are only by-products. Therefore, a Brüel and Kjaer accelerometer (type 4368) was used as a vibration pick-up system. The accelerometer, screwed to a 6.5 cm probing rod, was placed close to the crab's burrow and was connected to an Uher tape recorder (type 4200 Report Stereo IC) via a small preamplifier designed by the Institute of Applied Physics, Marburg (Dr. K.H. Wittich). The recordings were analysed in Marburg by examination of oscillograms obtained from a Philips oscilloscope PM 3231 in combination with a camera (Tönnies Recordine K-854).

The soil temperature ranged from 23 to 27.5 °C during the recordings (including the ones in Marburg). All crab individuals tested were of medium size when compared with the figures of maximum carapace width for each species (contained in Fig. 2). No special attempts were made to detect signals of females, which tend to be rare and more faint, when present (von Hagen 1984). Thus all data given in this paper refer to males. Mean values of the signals recorded were compared by a version of Student's t-test for heterogeneous variances and unequal sample sizes (L-test, Graf *et al.* 1966; cf. Zöfel 1992).

RESULTS

Main types of sounds. Nearly all of the signals analysed in this paper were recorded in an agonistic context, i.e. the accelerometer was placed close to the mouth of a burrow occupied by a crab ("owner"). A conspecific ("intruder") wandering about in the aquarium either detected the burrow spontaneously or was placed into the mouth of the burrow by the experimenter. In many of these situations one or both crabs emitted vibration signals, sometimes in an antiphonal manner (i.e. duetting with alternation). Sounds were either single ones or sequences of sounds (Fig. 1).

Most of the species tested (though not all) produced the usual percussive or rapping sounds or "rolls" of the

major cheliped, called "drumwhirls" in this paper and also by Salmon and Atsides (1968) and by Crane (1975), who also speaks of "major-manus-drum".

All species emitted signals that are regarded as "additional components" of acoustic behaviour (von Hagen 1984) and are, like respiration noises, normally not specifically searched for by investigators. These signals, called "bounces" in this paper and "leg-flicking" by Salmon and Horch (1972), are "hoarse" burst-pulsed sounds that correspond to laterally directed jerks of the whole animal during its subterranean approach towards an opponent, often in a "testing" manner. These sounds are produced by the joint jerking motion of the flexed ambulatories and are rather irregularly shaped and spaced (e.g. Fig. 1 vm). By contrast, the drumwhirls of the major cheliped are highly stylized and "elaborate" signals (e.g. Fig. 1 sg) and are used not only in agonistic encounters, but also as courtship display.

"Bounces" (burst-pulsed sounds). Examples of sequences of bounces produced by *H. cordiformis* and *U. vomeris* are given in Figure 1 (Hc, vm; cf. Table 2). Bounces seem to form the only acoustic signals detectable in these two species and *U. dampieri* (not figured), though in *H. cordiformis* the bounces may be superimposed by more evenly shaped short ambulatory "trills", visible in the first and last signal of Figure 1 Hc and probably identical with the "ambulatory tapping" that Griffin (1968) observed in the field.

Bounces were found in all species of *Uca* studied, though not figured in all cases. Bounces (most often a single one) frequently precede drumwhirls (Fig. 1 hs₁, ds₂, fl₂, cc, rs, mb, pp, an), especially in the species of group V ("*Celuca*").

Some species (in addition to *H. cordiformis*, *U. vomeris* and *U. dampieri*) produce bounces in short or long sequences. Such sequences occur at least in *U. seismella*, *U. coarctata*, *U. mjoebergi* and *U. annulipes* (Fig. 1 ss₁, cc₁, mb₁, an₁). Of these, the Australian species

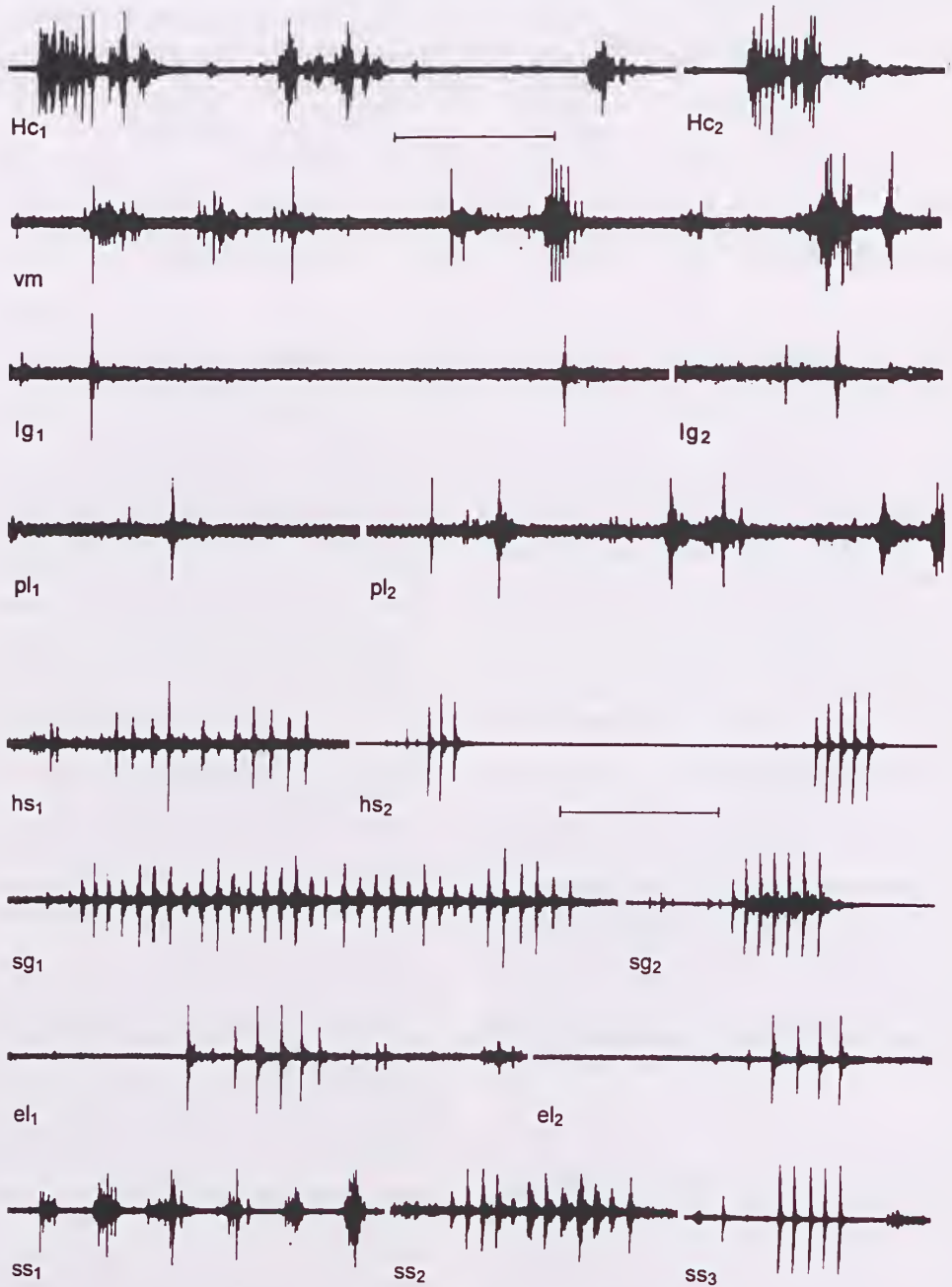


Fig. 1. Oscillographic samples of vibration signals of Australian *Uca* species, two Asian species (*U. rosea*, *U. annulipes*) and *Heloeccius cordiformis*. Explanation of species name abbreviations given, in same order, in Table 1. Scale bars 0.5 seconds. Following part of legend lists type and number of signals: B, bounces; D, drumwhirls (with number of strokes in parentheses): *Hc*₁ and *Hc*₂, 4 B, first and last superimposed by ambulatory trills. - *vm*, 8 B. - *lg*₁, 2 D (1 each); *lg*₂, D (2). - *pl*₁, D (1); *pl*₂, 3 D (2 each). - *hs*₁, B + D (15); *hs*₂, 2 D (7 and 8).

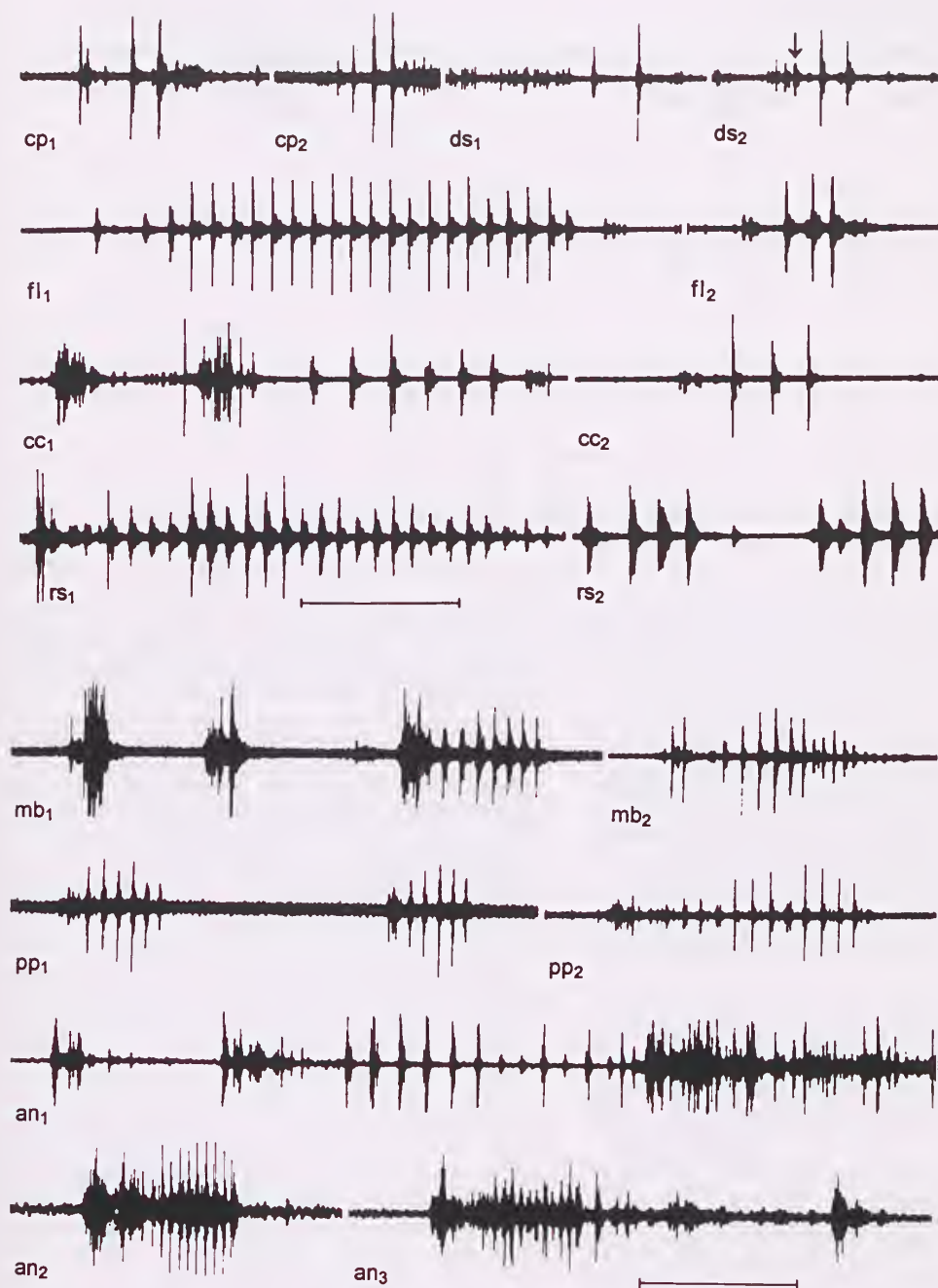


Fig. 1 (cont.): Oscillographic samples of vibration signals. - *sg*₁, D (35); *sg*₂, D (14), (both from Darwin). - *el*₁, D (9); *el*₂, D (6). - *ss*₁, 6 B; *ss*₂, D (12); *ss*₃, D (5). - *cp*₁, D (4); *cp*₂, D (4). - *ds*₁, D (2); *ds*₂, B + D (3), arrow points to first stroke. - *fl*₁, D (21); *fl*₂, B + D (3). - *cc*₁, 2 B + D (6); *cc*₂, B + D (3). - *rs*₁, B + D (26); *rs*₂, D (5) + B + D (3). - *mb*₁, 3 B + D (7); *mb*₂, B + D (16). - *pp*₁, B + D (6) + B + D (5); *pp*₂, B + D (12). - *an*₁, 2 B + D (14) + continuous ambulatory trill; *an*₂, B + D (10); *an*₃, B + D (13) + B.

Table 3. Rapping sounds of Australian male fiddler crabs (results of oscillographic analysis of tape recordings, cf. Fig. 1). W, E: Samples from western and eastern populations, respectively.

Species of <i>Uca</i>	One (complex) sound ("drumwhirl"); seconds		One sound plus subsequent silent interval: seconds		Strokes per sound: number			Period (one stroke plus subsequent pause): milliseconds		Number of sounds measured (males)	
	mean	s.d.	mean	s.d.	mean	s.d.	range	mean	s.d.		
<i>longidigitum</i>	0.18 ± 0.16		1.33 ± 0.34		1.87 ± 0.87		(1-4)	159 ± 34		23	(3)
<i>polita</i>	0.12 ± 0.12		1.39 ± 0.63		1.58 ± 0.77		(1-5)	163 ± 40		36	(4)
<i>hirsutimanus</i>	0.45 ± 0.16		1.86 ± 0.75		10.09 ± 2.78		(5-16)	48 ± 5		43	(4)
<i>signata</i> (W)	0.90 ± 0.52		2.55 ± 0.84		22.03 ± 11.34		(7-45)	41 ± 4		35	(2)
<i>signata</i> (E)	1.03 ± 0.41		2.99 ± 0.63		20.22 ± 7.09		(8-38)	53 ± 4		23	(3)
<i>elegans</i>	0.36 ± 0.17		2.11 ± 1.07		7.30 ± 2.75		(2-11)	54 ± 12		20	(3)
<i>seismella</i>	0.36 ± 0.14		1.17 ± 0.44		8.05 ± 2.58		(5-14)	49 ± 3		37	(4)
<i>capricornis</i>	0.22 ± 0.13		1.71 ± 0.41		3.10 ± 0.97		(2-5)	90 ± 23		20	(3)
<i>dussumieri</i>	0.12 ± 0.04		3.24 ± 1.04		2.06 ± 0.44		(1-3)	98 ± 25		16	(4)
<i>flammula</i>	0.84 ± 0.53		2.36 ± 0.77		13.40 ± 8.89		(2-33)	69 ± 12		57	(5)
<i>coarctata</i>	0.32 ± 0.19		1.91 ± 0.58		3.33 ± 1.88		(1-11)	136 ± 27		27	(3)
<i>mjoebergi</i>	0.49 ± 0.23		2.33 ± 0.80		9.42 ± 3.71		(4-21)	56 ± 6		64	(5)
<i>perplexa</i>	0.38 ± 0.23		1.85 ± 1.00		7.72 ± 3.43		(3-15)	52 ± 7		54	(5)

are included in Table 2, which presents some parameters measured. Table 2 is mainly meant to illustrate the specialized character of the bounces of *U. seismella* (cf. Fig. 1 *ss₁*). Long sequences of bounces (only comparable with those of *U. vomeris*) are an essential part of its acoustic communication. *U. seismella* is also conspicuous by its extremely low means and low standard deviations (differing from all other species, $p < 0.001$).

"Drumwhirls" (rapping sounds). Oscillographic examples of rapping sounds are given in Figure 1 for 14 species including the Asian forms *U. rosea* and *U. annulipes*. Three Australian species, namely *H. cordiformis*, *U. dampieri* and *U. vomeris*, never emitted rapping sounds.

Numbers of strokes listed in the legend of Figure 1 were verified by the running tape; the sudden extreme decrease of pulse amplitude (e.g. Fig. 1 *hs₂*, *el*, *mb₂*, *an₁*) is due to reduced contact between chela and substratum.

Time patterns of the Australian species are to be found in Table 3. The means given in this table are partly based on up to five males (see last column of Table 3) and different localities (Table 1). They have been united after testing their statistical compatibility. In *U. signata*, samples from Darwin and Cairns had to be treated separately (see below). Species with small numbers of sounds recorded (Table 3) reflect rarity of sound production (*U. longidigitum*, *U. capricornis*, *U. dussumieri*) or faintness of signals (*U. elegans*). Figure 2 and Table 4 were prepared to facilitate comparisons within Table 3. The results can be summarized as follows:

1) *Relations of body size and repetition rate of strokes.* As the repetition rate of the rapping elements

(strokes per second, calculated from the period in Table 3) might simply reflect the species-specific body size, the species were arranged according to the maximum carapace width recorded for Australia (Fig. 2, left scale and open circles). This arrangement is in accord with the systematic grouping of Table 1.

As expected, the repetition rates (Fig. 2, right scale and filled circles) mostly correspond to the body size (though inversely): the broken line drawn at 17 strokes per second divides the larger and thus "clumsier" and slower species of group I and II from the smaller and more agile species of group III and V. Within this scheme the top positions are held by *U. flammula* and the western *U. signata* sample, respectively. The two species confirm the advanced character of their acoustic signals also by the high number of strokes per sound (Table 3 and Fig. 1 *sg₁*, *fl₁*).

On the other hand, the repetition rates of *U. longidigitum* and *U. polita* do not fit the scheme at all: the two species have the lowest repetition rates, though they belong to the smaller species (middle and right sections of Fig. 2). The exceptional status of the two species is stressed by their low number of strokes per sound (Table 3 and Fig. 1 *lg*, *pl*). For a weighting of these characters see below (Discussion).

2) *In search of effects of allopatry and sympatry.* Most of the 17 confirmed Australian species of *Uca* are confined to one of the two northern zoogeographic provinces: the Dampierian in the west and the Solanderian in the east, seen from the Torres Strait region (von Hagen and Jones 1989; cf. Table 1 of the present paper). Some of these allopatric species are still similar, i.e. they form inter-provincial pairs or groups of relatives. The

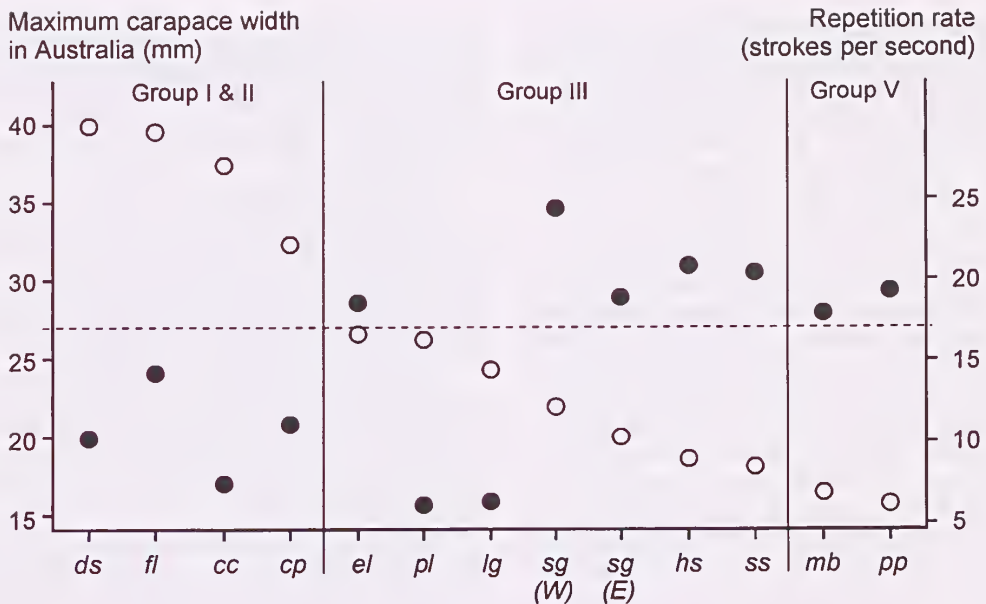


Fig. 2. Body size (left scale, open circles) and repetition rate of rapping strokes (right scale, filled circles) in 12 species of Australian *Uca* (abbreviations of species names and Roman group numerals as in Table 1). Values of *U. signata* separated according to a western (W) and eastern (E) sample. Maximum carapace widths in Australia after George and Jones (1982), except for *U. seismella* (Karumba sample of author). Repetition rate calculated from the period of strokes in Table 3.

Table 4. Statistical comparison of allopatric and sympatric relatives (*Uca* spp.) and populations of *U. signata* (W western, E eastern) using two parameters of Table 3. ***, **, *: differences significant: $p < 0.001$, < 0.01 , < 0.05 , respectively; n.s. not significant (L-test). See Table 1 for geographic distribution of the species mentioned.

			Strokes per sound	Period of strokes
<u>Allopatric relatives:</u>				
<i>U. capricornis</i>	vs.	<i>U. dussumieri</i>	***	n.s.
<i>U. capricornis</i>	vs.	<i>U. coarctata</i>	n.s.	***
<i>U. flammula</i>	vs.	<i>U. coarctata</i>	***	***
<i>U. mjoebergi</i>	vs.	<i>U. perplexa</i>	*	**
<u>Sympatric relatives:</u>				
<i>U. longidigitum</i>	vs.	<i>U. polita</i>	n.s.	n.s.
<i>U. elegans</i>	vs.	<i>U. hirsutimanus</i>	***	*
<i>U. seismella</i>	vs.	<i>U. polita</i>	***	***
<i>U. capricornis</i>	vs.	<i>U. flammula</i>	***	***
<i>U. dussumieri</i>	vs.	<i>U. coarctata</i>	**	***
<u>Populations of <i>U. signata</i>:</u>				
<i>U. signata</i> (W)	vs.	<i>U. signata</i> (E)	n.s.	***
<i>U. signata</i> (W)	vs.	<i>U. hirsutimanus</i>	***	***
<i>U. signata</i> (E)	vs.	<i>U. hirsutimanus</i>	***	***
<i>U. signata</i> (W)	vs.	<i>U. elegans</i>	***	***
<i>U. signata</i> (E)	vs.	<i>U. elegans</i>	***	n.s.

four species (*U. polita*, *U. signata*, *U. seismella*, *U. triangularis*) that occur in both provinces appear to have extended their range secondarily. They are one reason for the fact that close relatives occur not only in allopatric but also in sympatric distribution (Table 4).

It is to be expected that allopatric relatives are rather "careless" of evolving species-specific vibration signals: there is no selection against retaining signals that antedate geographic separation. In fact three of the four allopatric pairs listed in Table 4 are similar (differences n.s. or $p < 0.05$ only) in one of the parameters chosen for comparison (strokes per sound and period of strokes).

Sympatric relatives should reinforce selectivity of their communication system, and the frequency of significant differences in both parameters mainly appears to fit this concept (Table 4). The pair *U. longidigitum* vs. *U. polita* (Table 4) forms a puzzle, as both species are reported from Sandgate and Shorncliffe in Moreton Bay near Brisbane (George and Jones 1982). In 1986 the author found the two species at Shorncliffe on the same mud-flat opposite to the mouth of Nundah Creek, but not a single individual of *U. polita* in the many *longidigitum*-habitats of the Brisbane River itself. Though both are members of the Solanderian province, the two species seem to meet rarely in the field so that their different time pattern of waving display (Pellikan 1990) may be sufficient as a behavioural isolating mechanism.

The western and eastern samples of *U. signata* (from Darwin and Cairns) were treated separately throughout the paper, because they had clearly different periods of strokes ($p < 0.001$, Table 4). Each population of *U. signata* was compared with the two related western (Dampierian) species *U. hirsutimanus* and *U. elegans*. Indications of character displacement (i.e. the same two species differ more in sympatry than in allopatry) were not found between *U. signata* and *U. hirsutimanus*, but between *U. signata* and *U. elegans* (Table 4). The latter may be the closest relative of *U. signata* (Pellikan 1990).

3) *Comparison with signals of two Asian species.* The two *Uca* species of South East Asia that were included in this study fit easily into the systematic grouping of the Australian species (Table 1). However, within these groups the Asian species appear to be more specialized.

The number of strokes in isolated sounds of *U. rosea* (e.g. 26 in Fig. 1 rs_1 ; mean 17.06 ± 6.08 , $n = 17$ drumwhirls of this long type) is only comparable with that of *U. flammula* (Table 3). There are shorter sounds in both species (Fig. 1 fl_1 , rs_2), but only *U. rosea* can "switch" to long sequences of short drumwhirls (up to 12 sounds measured, instead of up to 3 in *U. flammula*).

Likewise, *U. annulipes* is more specialized than the two related Australian species *U. mjoebergi* and *U. perplexa*. The number of strokes per sound is similar to that of *U. mjoebergi* and *U. perplexa*, but the period of strokes is more variable (cf. an_1 with an_2 and an_3 in Fig. 1). In *U. annulipes* the drumwhirls are often followed (or preceded) by continuous burst-pulsed "trills" (Fig. 1 an_1) of the walking legs, lasting up to about ten seconds. These trills were also recorded in *U. perplexa*, but more rarely, and they appear to be missing in *U. mjoebergi*.

DISCUSSION

In explaining the Figures and Tables in the section on "drumwhirls", a few conclusions were attempted that are more or less well supported. It is clear that body size and repetition rates of strokes are inversely related (with a few striking exceptions), but the second idea that sympatry and allopatry should influence the signals needs to be tested by closer pair-by-pair examinations (cf. von Hagen 1984). A more detailed study of the *U. longidigitum*-*U. polita* pair and of the western and eastern populations of *U. signata* should be especially rewarding. Work on *U. signata* should also include samples from New Guinea, where the species occurs at least around Merauke, Irian Jaya (Leiden Museum, Netherlands: e.g. No. D32522, D33526; von Hagen unpublished).

It is also premature to make general conclusions on the advanced status of the signals of Asian fiddler crabs (see third section). The two species chosen (*U. rosea*, *U. annulipes*) might be specialized species by chance. There exist, however, some additional bioacoustic data:

of *U. paradussumieri* Bott (= *U. spinata* Crane) and *U. dussumieri* from Malaysia and Indonesia (R. Polivka pers. com.). Judging only from their range of stroke numbers per sound (3 - 21 and 2 - 6, respectively) these Asian forms, too, appear to be more advanced than their Australian relatives.

As is evident from examination of Figure 1 and Table 3 the sounds of Australian *U. dussumieri* as well as of *U. capricornis* and *U. coarctata* are among the simplest signals recorded. These species apparently hold a basal position within the "*Deltnca*"-group, with regard to its Australian as well as to its Asian members.

Only members of *Australuca* (group III), namely *U. longidigitum* and *U. polita*, are even simpler with respect to their signals: by their mean number of strokes (minimum in Table 3) and their long stroke period (maximum in Table 3, resulting in an exceptional low repetition rate, Fig. 2).

Especially *U. longidigitum* (Fig. 1, lg), with the distribution pattern of a relict species (see George and Jones 1982), could have preserved the earliest phylogenetic stage of drumwhirl invention in *Uca*, namely rapping as a by-product of waving the major cheliped. Within *Anstraluca*, *U. longidigitum* is the only species in which the length of one sound plus subsequent interval (1.33 ± 0.34 , $n = 23$, Table 3) is statistically not separable from the length of one waving motion plus subsequent pause (1.22 ± 0.11 , $n = 36$, according to motion pictures taken by the author and analysed by Pellikan 1990). Even in the aquarium *U. longidigitum* tended to switch from waving to rapping (and vice versa), the latter looking like a reduced or weak waving movement.

Vibration components of visual display are well-known in *Uca* (Altevogt 1964), but in *U. tangeri*, a species that also possesses a complete system of drumwhirls, *U. longidigitum* seems to have but one gesture that serves two sensory channels - depending on its intensity or completeness. It is important to note that the nearly all Australian "*Anstraluca*"-group (which includes *U. longidigitum*) retains, as a whole, some other ancestral traits: above all, minor chelae with large teeth (Crane 1975) and waving display of females (von Hagen 1993).

It is not clear, whether the "*Thalassuca*"-group, which also has waving females (von Hagen 1993), holds a still more ancestral position with regard to sound evolution in *Uca*. The two Australian members, *U. dampieri* and *U. vomeris*, never emitted drumwhirls within the experimental design of the present study, though they should have: Crane (1975) recorded, in the field, underground rapping sounds in the close relatives *U. hesperiae* from East Africa and *U. pacifensis* from Fiji (see her Plate 47 A) and even in *U. vomeris* from New Caledonia; and Salmon (1984) describes a "shuttling" motion of the major chela in *U. vomeris* from Townsville,

used by intruders in the entrance of another crab's burrow. A gesture of this kind was filmed in Cairns in a male of *U. vomeris* fighting on the surface of the ground (von Hagen, unpublished). Furthermore, the American narrow-fronts (*Uca sensu stricto*) are thought to be a branch of "*Thalassuca*" (Crane 1975), and they have genuine drumwhirls (e.g. von Hagen 1971, 1972).

However, even without certainty in the case of *U. dampieri* and *U. vomeris*, Australia remains the continent where all stages of sound evolution are to be found: *H. cordiformis* without drumwhirls, *U. dampieri* and *U. vomeris* apparently without proper drumwhirls or normally not using them underground, *U. longidigitum* and *U. polita* with drumwhirls of a very early stage, *U. capricornis*, *U. dussumieri* and *U. coarctata* with simple sounds not much more progressive than those of *U. polita*, and after an intermediate stage two especially advanced positions, which evolved independently out of *Australuca* (*U. signata*) and "*Deltuca*" (*U. flammula*). Among the intermediate forms (not specified here) two species have, in addition to their drumwhirls, evolved peculiarities: *U. seismella* has specialized in long sequences of "hasty" bounces and *U. perplexa* (like *U. annulipes*) in continuous ambulatory trills.

Housing all stages of sound evolution, especially the early ones, and also the early stages of waving evolution (von Hagen 1993), Australia should be favoured as the continent where the genus *Uca* first evolved.

The author is aware that directional change in behavioural complexity cannot be the only indicator in phylogenetic reasoning. A support at least by morphological studies is necessary (Beinlich and von Hagen in prep.). However, this holds true also for other approaches. Two related papers, which were published some years ago (Levinton *et al.* 1996, Sturmbauer *et al.* 1996), base their phylogenetic trees on certain analyses of 16S rDNA alone. Their inferences, above all an American centre of origin of *Uca*, should be treated with reserve, as they lack a proper morphological background for their discussions, which neglect for example, the most reliable synapomorphy in *Uca* systematics: the unique pleonal clasping apparatus identifying all broad-fronted species as a monophylum (Guinot 1979, Beinlich and von Hagen in prep.).

The assumption that *Uca* first evolved in Australia is, furthermore, supported by an Australian origin of certain mangrove taxa (palynological evidence compiled in Specht 1981). As *Uca* is typically associated with mangroves, it is essential that *Rhizophora*, *Avicennia* and *Sonneratia* first appeared in the late Eocene of West Australia and colonized Indonesia not before Oligocene/Miocene - probably accompanied by fiddler crabs, which made South East Asia not their first, but their second centre of evolution. Crane, who considers "*Deltuca*" the subgenus "least specialized" (Crane 1975) and at first supposed a Malaysian origin of the genus (Crane 1956),

finally called Australia's northwest coast "the most conservative area, judging by the morphology of the local *Uca*" (Crane 1975). As the east coast has its ancestral forms as well (*H. cordiformis*, *U. longidigitum*, *U. coarctata*), one should extend Crane's assessment to the whole continent.

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Caetrathynnus, *Nitidothynnus* and *Procerothynnus*, new genera of Thynninae (Hymenoptera: Tiphidae) from northern Australia

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ABSTRACT

Three new genera are erected to accommodate nine new species of thynnine wasps: *Caetrathynnus* for *C. greggi* sp. nov. (type species), *C. galbinus* sp. nov. and *C. wesselensis* sp. nov.; *Nitidothynnus* for *N. purdiei* sp. nov. (type species), *N. ebeneus* sp. nov. and *N. spinulus* sp. nov.; and *Procerothynnus* for *P. centralianus* sp. nov. (type species), *P. arthemius* sp. nov. and *P. carpentarianus* sp. nov. All the new species are described from males only, except *Nitidothynnus spinulus* and *N. purdiei*, which are known from both males and females. Keys to species are given, as is a discussion of coupling mechanisms in *Nitidothynnus* and the phenomenon of mixed species couples is considered in light of the biology of the subfamily. Most of the new species are recorded only from the Top End of the Northern Territory, although *Caetrathynnus galbinus* also occurs in adjacent areas of northern Western Australia and *Procerothynnus carpentarianus* also occurs in adjacent areas of north-western Queensland. *Procerothynnus centralianus* is recorded from central Australia while *Nitidothynnus ebeneus* is known only from the holotype from northern Queensland.

KEYWORDS. Tiphidae, Thynninae, new genera, *Caetrathynnus*, *Chilothynnus*, *Nitidothynnus*, *Procerothynnus*, *Aspidothynnus*, Australia, taxonomy, biogeography.

INTRODUCTION

Wasps of the subfamily Thynninae comprise a very diverse group in Australia which includes many undescribed species and genera (Brown 1998a). Some 600 species have been described, mostly from the vicinity of the large coastal cities in eastern, south-eastern and south-western mainland Australia (Given 1954; Salter 1954). Very few have been described from northern or inland Australia, and there are only 26 known from the Northern Territory.

Adults are most commonly observed feeding on flowers (hence the common name "flower wasps") where they often occur in copula. The main food source appears to be nectar, although other plant and insect secretions and exudates are also eaten (Tillyard 1926; Burrell 1935). Nectar from flowers of the plant family Myrtaceae, which includes eucalypts and tea trees, is particularly attractive, and may attract these wasps in large numbers at the height of the flowering season.

Male thynnines are fully-winged, while females are smaller, wingless, and somewhat ant-like in appearance. Because females are wingless, and cannot therefore travel very far by themselves, they are dependant on males for food. Feeding occurs during mating as pairs

couple for long periods during which the male carries the female to flowers. Pairs remain coupled while both are feeding, and there are morphological structures present that assist pairs to remain coupled for prolonged periods. Since the sexes are so different morphologically, it is the convention to describe each separately. Unfortunately in the descriptions that follow this is not possible for every species because of the lack of females.

Females produce pheromones to attract males prior to mating. However, on rare occasions when a conspecific male never arrives, a female may couple with a non-conspecific male (Brown 1993). This is a common occurrence in this subfamily and is most probably a mechanism that ensures a hungry female is carried to a food source at the expense of successful mating. The latter may be of little concern to the survival of the species as a whole because unfertilised females of all Hymenoptera (ants, bees and wasps) produce male offspring which are haploid anyway (Naumann 1991). This phenomenon of misecoupling is mentioned specifically under the descriptions of *Nitidothynnus purdiei* and *N. spinulus* in this paper.

The Thynninae has not been revised taxonomically since 1910 (Turner 1910) and the only critical examinations since then have been revisions for the

genera *Acanthothynnus* Turner, *Doratithynnus* Turner, *Encopothynnus* Turner and *Macrothynnus* Turner (Brown 1987, 1989a, 1989b, 1995a). These revisions indicated that, in at least these genera, between 50% and 75% of the fauna currently represented in collections was undescribed and that many species were known from only one or two specimens. This suggests that more extensive collecting, especially in more remote areas such as the Northern Territory of Australia, will reveal even more new species.

Currently there are 37 genera considered to be valid within the tribe Thynnini in Australia (Given 1954; Brown 1983, 1992, 1995b, 1997a, 1997b, 1998b). Studies by the present author indicate that these genera form three distinct clusters. The first cluster contains the genera *Bifidothynnus* Brown, *Campylothynnus* Turner, *Catocheilus* Guérin, *Elidothynnus* Turner, *Guerinius* Ashmead, *Leptothynnus* Turner, *Lestricothynnus* Turner, *Lophocheilus* Guérin, *Macrothynnus* Turner, *Megalothynnus* Turner, *Oncorhithynnus* Salter, *Pogonothynnus* Turner, *Thynnoides* Guérin, *Thynnus* Fabricius and *Zaspilothynnus* Ashmead. It is distinguished from the other two generic clusters by numerous characters including the labrum weakly rather than strongly narrowed basally, the propodeum oblique in profile, tergite 7 longitudinally multicarinate (except in *Bifidothynnus* and *Guerinius* which have tergite 7 otherwise modified) and sternite 8 with prominent basal angles or spines in the male, and sternite 5 rugose and/or carinate in the female. Most Australasian species are also larger in size than those found in the other two clusters.

The second cluster includes *Acanthothynnus* Turner, *Arthrothynnus* Brown, *Aspidothynnus* Turner, *Doratithynnus* Turner, *Encopothynnus* Turner, *Epactiothynnus* Turner, *Gymnothynnus* Turner, *Iswaroides* Ashmead and *Tuesothynnus* Turner. It differs from the subsequent cluster by having most metasomal segments strongly constricted (and sometimes spinose), and tergite 7 with a strong transverse apical carina.

The third generic cluster includes *Aeolothynnus* Ashmead, *Agriomyia* Guérin, *Ariphrou* Erichson, *Chilothynnus* Brown, *Leiothynnus* Turner, *Neozeleboria* Rohwer, *Pentazeleboria* Brown, *Phyuatothynnus* Turner, *Psaumothynnus* Ashmead, *Tachynoides* Kimsey, *Tachynomyia* Guérin, *Tachyphrou* Brown, and *Zeleboria* Saussure. This cluster is distinguished from other Australian Thynnini (and Thynninae) by the combination of: a relatively short, weakly protruding sternite 8 that is not broadened into lobes or spines at the base, and which may be armed apically with a narrow spine (with or without lateral spines); the metasomal segments are not strongly constricted or heavily sclerotized; a convex tergite 7 that is uniformly punctate

with a medial impunctate area, but without a transversely carinate apical margin; and the basiparameres are not strongly developed ventrobasally such that the ventro-basal angle (in profile) is well separated from the basal ring. A key to genera in this cluster was given by Brown (1998a), although *Tachynoides* was omitted. That genus keys to *Tachyphrou* in that key.

The three new genera described here belong to the third cluster. Two of these were included in the key to genera by Brown (1998a) and referred to as genus A and genus B.

Terminology follows Snodgrass (1941), Brown (1997a,b) and Naumann (1991). Relative terms relating to microsculpture are interpreted as follows: sparsely punctate = punctures greater than two puncture-diameters apart; punctate = punctures at most two puncture-diameters apart, but never confluent; closely punctate = punctures almost confluent; rugosely punctate = punctures partially confluent; finely punctate = punctures small and shallow; coarsely punctate = punctures large and deep; obscurely punctate = punctures small, sparse, shallow and only visible at certain angles.

Abbreviations. Morphological characters: T1-7, metasomal tergites 1-7; S1-8, metasomal sternites 1-8; POL:OOL, ratio of distance between posterior ocelli to distance between eye and posterior ocellus. Specimen repositories: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, CSIRO, Canberra; BMNH, The Natural History Museum, London; MV, Museum of Victoria, Melbourne; NTM, Museum and Art Gallery of the Northern Territory, Darwin; OTTAWA, Agriculture Canada, Ontario; QM, Queensland Museum, Brisbane; SAM, South Australian Museum, Adelaide; UQIC, University of Queensland, Brisbane; WAM, Western Australian Museum, Perth.

SYSTEMATICS

Caetrathynnus gen. nov.

Type species. Here designated *Caetrathynnus greggi* sp. nov.

Generic diagnosis. *Male.* Head, mesosoma and metasoma strongly polished with metasoma shagreened. Mandibles long, narrow and straight. Clypeus convex, strongly produced and broadly truncate apically. Antennal prominence long, narrowly U-shaped with margins slightly emarginate dorsally, sagittally sulcate, and with short oblique carina above antennal insertions. Frons strongly and broadly depressed lateral to antennal prominence. Antennae short and only just reaching propodeum, apical 6 segments weakly arcuate. Pronotum with anterior margin weakly raised not carinate, lateral margins strongly convergent anteriorly. Mid femur strongly and abruptly broadened at base. Metasoma

fusiform, segment 1 subpetiolate, about as wide as long; segments 3-4 widest, segments (apart from T2 and S2 anteriorly) not constricted. T7 convex, slightly produced and membranous apically, not transversely apical carinate. S8 subtriangular with a single narrow slightly upturned apical spine, narrowly emarginate at base of spine. Genitalia with basal ring cylindrical, not short; basiparameres suborbicular to subtriangular (viewed dorsally), not apically emarginate; parameres subparallel, of moderate length and width, apex subtruncate; cuspides of moderate length with opposing digitate digitus apically.

Remarks. *Caetrathynnus* is most readily distinguished from other thynnine genera (in particular, those of the third cluster) by the structure of the mandibles which are long, narrow and straight, and the clypeus which is broadly convex without a sagittal carina, and with the apical margin strongly produced and broadly truncate. The broadly convex and broadly apically truncate clypeus suggests a relationship with *Psammothynnus* and *Zeleboria*. However, in both of these genera, the mandible is shorter, broader and curved (as normally found in other genera) and the clypeus is shorter, more strongly convex and sagittally carinate. These differences in clypeal shape suggest that an enlarged clypeus may have arisen in *Caetrathynnus* independently to that of *Psammothynnus* and *Zeleboria*, and is supported by differences in the genitalia which differ from *Caetrathynnus* by having the basal ring very short, the fused basiparameres truncate to emarginate dorsoapically and, in many species, the parameres with a ventroapical lobe. These two genera also lack a single medial spine on S8 which occurs in *Caetrathynnus* and many other Thynninae.

Caetrathynnus superficially resembles *Aspidothynnus* Turner in that: the clypeus is broadly convex, and strongly and broadly produced apically without a sagittal carina; and the metasoma is fusiform without spines on the tergites or sternites. However, *Aspidothynnus* belongs to the second generic cluster and as such differs by those characters as listed in the Introduction. *Aspidothynnus* also differs from *Caetrathynnus* by having the antennal prominence weakly developed rather than long, narrowly U-shaped with margins slightly emarginate dorsally; T1 wider than long rather than as approximately as wide as long; and metasomal segments with spots rather than lunulate marks.

The three species of *Caetrathynnus* are very similar in appearance, but differ slightly in the punctuation of clypeus, gena and pronotum, and the shape of the fore coxae, the depth of the anterior depression on S2 (typical of all Thynninae), the base of the apical spine of S8, and the genitalia. They are reliably distinguished by the genitalia.

All three are recorded from the north of the Northern Territory. *Caetrathynnus galbinus* sp. nov. is recorded from near the Western Australian border while *C. wesselensis* sp. nov. is known only from the holotype from the Wessel Islands. *C. greggi* sp. nov. is the most widely occurring species, and it ranges from Darwin to Borroloola.

Caetrathynnus was referred to as genus "A" by Brown (1998a) in a key to closely related genera.

Etymology. The generic name is masculine and is derived from the Latin word *caetra* (also spelt *cetra*) which is a type of shield. It is a reference to the shape of the male clypeus.

Key to males of *Caetrathynnus*. (Females are unknown.)

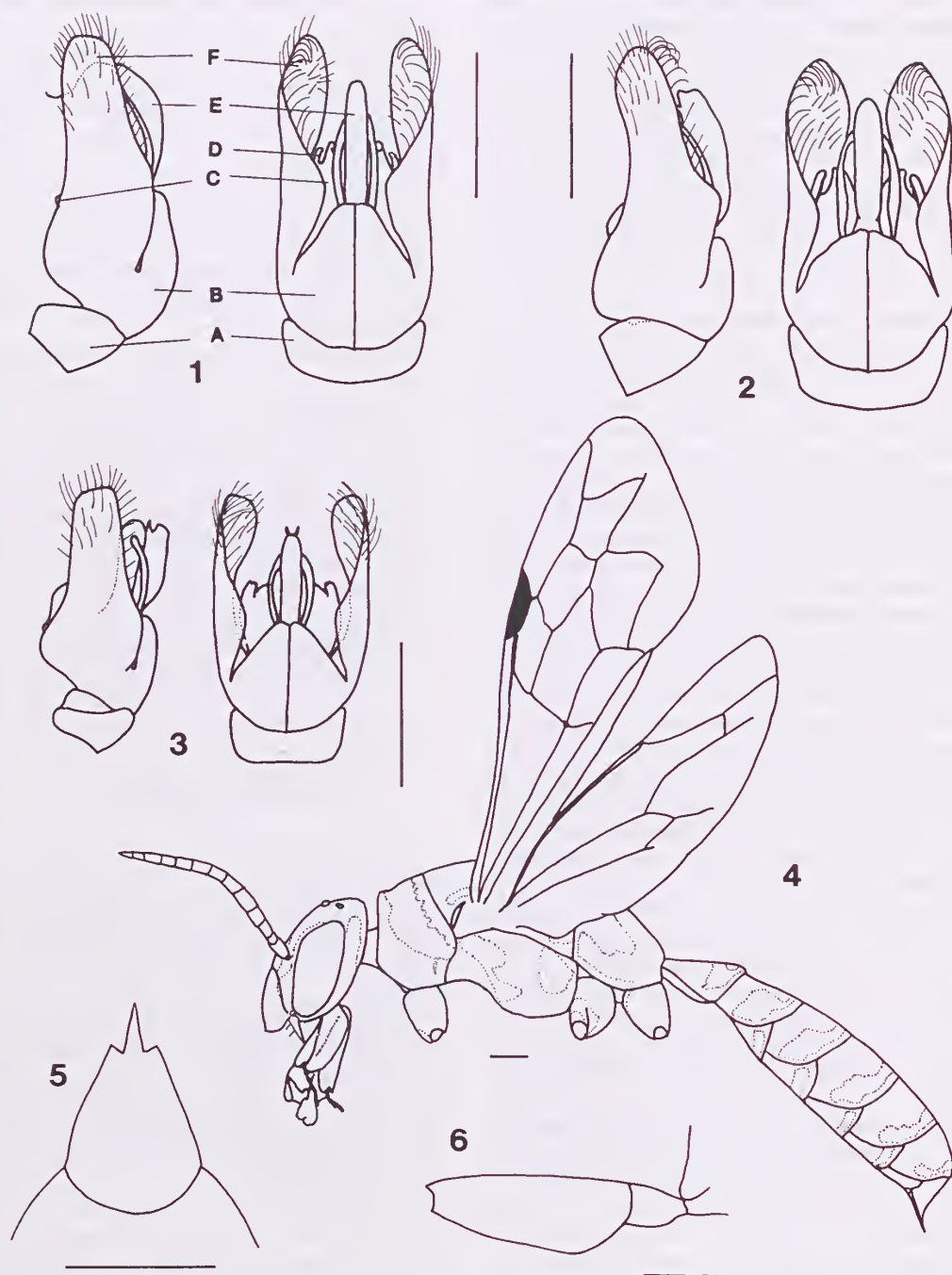
1. a Most sclerites predominantly yellow; prosterna black with yellow spot; propodeum with U-shaped lateral marks at least partially fused medially *C. galbinus* sp. nov.
- b Sclerites predominantly black (may have extensive yellow marks but not distinctively more yellow than black); prosterna black without yellow spot; propodeum with U-shaped lateral marks not fused medially 2
2. a Apex of parameres truncate (Fig. 3); base of cuspis sinusoidal (in profile) *C. wesselensis* sp. nov.
- b Apex of parameres rounded (Fig. 2); base of cuspis rounded (in profile) *C. greggi* sp. nov.

Caetrathynnus galbinus sp. nov.

(Fig. 1)

Type material. HOLOTYPE ♂ - NTM (1911): Keep River NP, Garrandalng, 15°53'S, 129°03'E, Northern Territory, 30 April 1996, G.R. Brown. PARATYPES - Western Australia: UQIC (3♂), 14 mi. (22.5 km) S of Kununurra, on *Eucalyptus ?pruinosa*, 5 March 1973, E.M. Exley.

Description of male. Body length 11 mm; fore wing 8 mm; hind wing 6 mm. Clypeus rugosely punctate, punctures shallow and vertically aligned, apical margin width to maximum width 1:2.0. POL:OOL 1:1.1. Frons closely and shallowly punctate. Vertex obscurely punctate. Gena shallowly and closely punctate. Pronotum sparsely and shallowly punctate, punctures more distinct posterolaterally. Mesoscutum and mesoscutellum sparsely punctate medially, closely punctate laterally. Metanotum punctate. Propodeum closely and shallowly punctate, punctures deeper laterally, impunctate anteriorly. Mesopleura closely to finely punctate. Fore coxae flat. T1 width to length 1:0.9. T2 weakly depressed anteriorly. Tergites and sternites closely and very shallowly punctate such that most tergites and anterior sternites almost appear impunctate, punctures coarser on posterior tergites. S1 not medially raised. S2 strongly



Figs 1-6. *Caetrathynnus* spp., males: 1, *C. galbinus* sp. nov., genitalia, lateral and dorsal; 2, *C. greggi* sp. nov., genitalia, lateral and dorsal; 3, *C. wesselensis* sp. nov., genitalia, lateral and dorsal; 4, *C. greggi* sp. nov., habitus; 5, *C. greggi* sp. nov., S8; 6, *C. greggi* sp. nov., right mid trochanter and femur. A, basal ring; B, basiparameres; C, cuspis; D, digitus; E, aedeagus; F, paramere. Scale lines = 0.5 mm.

depressed anteriorly. S8 slightly emarginate at base of spine. Genitalia as in Figure 1: basiparameres subtriangular (viewed dorsally) with each basiparamere truncate apically; parameres relatively short, subtruncate apically, weakly dorsally lobed (in profile) near base of aedeagus; cuspis subparallel basally, apically triangular, apex ending slightly beyond apex of digitus and outwardly curved, base rounded and slightly visible in profile.

Colour. Black; yellow colouration as follows: mandibles (except apex), stipes, clypeus (except obscure medial anchor-shaped mark), large longitudinal mark (except very narrow sagittal line) above antennal insertion, inner and outer orbits of eyes with outer orbit almost continuous with inner orbits and extending discontinuously across vertex, anterior margin of pronotum broadly (very narrowly discontinuous medially), posterior margin of pronotum broadly, tegulae, mesoscutum with large spot on disc and horizontal mark above fore wing, large spot on disc of mesoscutellum, axillae, metanotum, metapleuron, broad lateral U-shaped mark on propodeum, mesopleura (except mesopleural groove), spot on prosterna, margins of mesosternal lamellae, coxae (except base of mid and hind coxae), outer surfaces of trochanters, femora and fore tibiae, dorsal surface of fore femora, T1-6 (except anteromedially and posterolateral spot), sagittal line on S1, S2 (except anteromedial and posterolateral spots), curved lateral mark on posterior margin of S3-6 (almost confluent medially); orange colouration as follows: legs (except coxae outer surfaces of trochanters, femora and fore tibiae, dorsal surface of fore femora). Margin of tegulae semitransparent. Wing membranes hyaline with veins orange to brown. Setae white.

Distribution. Known only from the Northern Territory-Western Australian border near Kununurra.

Remarks. This species is distinguished from other species of *Caetrathynnus* by the extent of the yellow colouration such that most sclerites are predominantly yellow, including the presence of a spot on the prosterna, and enlarged U-shaped lateral markings on the propodeum which are at least partially fused medially. It is also distinguished by having the fore coxae flat, the clypeus with punctures vertically aligned, and the pronotum with punctures most distinct posterolaterally.

Yellow colouration may be expanded on the clypeus, and on the propodeum so that marks are confluent medially, or slightly reduced on the pronotum, propodeum and metasoma. Black on the metasoma may be partially replaced by brown, or it may be expanded such that it is confluent with the black posterolateral spots on some segments.

Etymology. The specific name is derived from the Latin word *galbinus* (= yellowish) and it refers to the extensive yellow colouration of the male.

Caetrathynnus greggi sp. nov.

(Figs 2, 4-6)

Type material. HOLOTYPE ♂ - NTM (1895): 17 Mile, Virginia, 12°33'S, 131°02'E, near Darwin, Northern Territory, 28 April 1996, S. Gregg. PARATYPES - *Northern Territory*: AM (K122050), BMNH (E2000-27), MV (T17352), NTM (1896-1898), QM (T57838), SAM (I 21437), WAM (26555) (9♂), same data as holotype (3 NTM, 1 AM), 4 May 1996 (1 BMNH, 1 MV), 19 May 1996 (1 QM, 1 SAM), December 1997 (1 WAM); NTM (1899-1901) (3♂), Arafura Swamp, 12°16'S, 124°59'E, 9 June 1996, G.R. Brown; NTM (1902-1903), OTTAWA (3♂), Berry Springs 50 km S Darwin, rainforest, Malaise trap, 4-27 December 1993, S. and J. Peck; ANIC (1♂), 12 km NNE of Borrooloola, 15°58'S, 136°21'E, 1 November 1975, J.C. Cardale; NTM (1904) (1♂), McMillans Rd [Berrimah] near Darwin, eucalyptus woodland, Malaise trap, 1-25 December 1993, S. and J. Peck; NTM (1905), OTTAWA (2♂), Berrimah near Darwin, mixed eucalyptus woodland, 25 December 1993-10 January 1994, S. and J. Peck; NTM (1906) (1♂), Mindil Beach near Darwin, 13 May 1996, S. Gregg; NTM (1907) (1♂), Melville I., swamp W of Taracumbi Falls, 11°35'S, 130°40'E, 4 October 1996, G.R. Brown and G. Dally; NTM (1908) (1♂), Melville I., Mirikau-Yunga Ck, 11°31'S, 130°41'E, 5 October 1996, G.R. Brown and G. Dally; NTM (1909) (1♂), Melville I., 11°35'S, 130°40'E, Malaise trap, 4-15 October 1996, G.R. Brown; NTM (1910) (1♂), Mt Mortgage, Humpty Doo, 12°35'S, 131°05'E, 28 February-31 March 1992, A. Wells and J. Webber; ANIC (1♂), 19 km NE of Mt Cahill, 12°47'S, 132°51'E, 16 November 1972, J.C. Cardale.

Description of male. Body length 8-12 mm; fore wing 6-9 mm; hind wing 4.5-6 mm. Clypeus rugosely and shallowly punctate, apical margin width to maximum width 1:1.6. POL:OOL 1:0.9. Frons closely and shallowly punctate. Vertex obscurely punctate. Gena shallowly and closely to rugosely punctate. Pronotum sparsely and shallowly punctate, punctures more distinct on anterior and posterior margins. Mesoscutum and mesoscutellum sparsely punctate medially, closely punctate laterally. Metanotum punctate. Propodeum closely and shallowly punctate, punctures deeper laterally, impunctate anteriorly. Mesopleura closely to finely punctate. Fore coxae almost flat. T1 width to length 1:1.0. T2 weakly depressed anteriorly. Tergites and sternites closely and very shallowly punctate such that most tergites and anterior sternites almost appear impunctate, punctures coarser on posterior tergites. S1 not medially raised. S2 depressed anteriorly. S8 emarginate at base of spine. Genitalia as in Figure 2: basiparameres broadly subtriangular (viewed dorsally) with each basiparamere rounded apically; parameres relatively long, rounded apically, distinctly dorsally

lobed (in profile) near base of aedeagus; cuspis subparallel basally, apically triangular, apex ending slightly beyond apex of digitus and outwardly curved, base rounded and strongly visible in profile.

Colour. Black; yellow colouration as follows: mandibles (except apex), clypeus (except medial anchor-shaped mark), large longitudinal mark (except very narrow sagittal line) above antennal insertion, inner and outer orbits of eyes almost continuous dorsally, transverse line behind ocelli, margins of pronotum (anterior margin very narrowly discontinuous medially, and expanded ventrally), tegulae, mesoscutum with large spot on disc and horizontal mark above fore wing, central and anterolateral spots on mesoscutellum, axillae, disc and anterolateral spot on metanotum, metapleuron, broad lateral U-shaped mark on propodeum, anterior vertical mark and small mark and adjacent spot near mid coxa on mesopleura, margins of mesosternal lamellae, coxae (except bases), extreme apices of femora, dorsal line on fore femora, ventral margin of mid and hind femora, lunulate lateral line on posterior margin of T1-6 and S3-5 usually or virtually contiguous medially; orange colouration as follows: legs (except coxae, apex of fore trochanter, extreme apices of femora, dorsal line on fore femora, ventral margin of mid and hind femora). Margin of tegulae semitransparent. Wing membranes hyaline with veins orange to dark brown. Setae white.

Distribution. Coastal Northern Territory from Darwin to Borroloola.

Remarks. This species is distinguished from *Caetrazygnus galbinus* by having less extensive yellow colouration such that most sclerites are predominantly black. It is distinguished from *C. wesselensis* sp. nov. by having the apex of the parameres rounded and the base of the cuspis rounded in profile. It is distinguished from both species by having S8 more emarginate at the base of the apical spine, the gena with punctuation more rugose, and the pronotum with punctuation more distinct on the anterior and posterior margins.

The yellow colouration may be expanded on the tergites to enclose a posterolateral spot, or reduced on the mesoscutum and mesoscutellum such that the medial spots are elongate marks. Black colouration on the trochanters may be replaced by orange.

Etymology. This species is named after Steven Gregg of the Museum and Art Gallery of the Northern Territory who collected many of the type series, and who has a great love of natural history.

Caetrazygnus wesselensis sp. nov.

(Fig. 3)

Type material. HOLOTYPE ♂ - ANIC : 11°01'S, 136°45'E, Rimbija Is., Wessel Islands, Northern Territory, 3-14 February 1977, T.A. Weir.

Description of male. Body length 7 mm; fore wing 6 mm; hind wing 4 mm. Clypeus rugosely and shallowly

punctate, apical margin width to maximum width 1:1.8, POL:OOL 1:0.9. Frons closely and shallowly punctate. Vertex obscurely punctate. Gena shallowly and closely punctate. Pronotum sparsely and shallowly punctate, punctures more distinct posterolaterally and ventrally. Mesoscutum and mesoscutellum sparsely punctate medially, closely punctate laterally. Metanotum punctate. Propodeum closely and shallowly punctate, punctures deeper laterally, impunctate anteriorly. Mesopleura closely to finely punctate. Fore coxae slightly convex. T1 width to length 1:1.2. T2 weakly depressed anteriorly. Tergites and sternites closely and very shallowly punctate such that most tergites and anterior sternites almost appear impunctate, punctures coarser on posterior tergites. S1 not medially raised. S2 depressed anteriorly. S8 slightly emarginate at base of spine. Genitalia as in Figure 3: basiparameres subtriangular (viewed dorsally) with each basiparamere rounded apically; parameres relatively short, distinctly truncate apically, weakly dorsally lobed (in profile) near base of aedeagus; cuspis subparallel basally, apically triangular, apex ending slightly before apex of digitus and not outwardly curved, base sinuate and strongly visible in profile.

Colour. Black; yellow colouration as follows: mandibles (except apex), clypeus (except obscure medial anchor-shaped mark), large longitudinal mark (except very narrow sagittal line) above antennal insertion, inner and outer orbits of eyes almost continuous dorsally, margins of pronotum (anterior margin narrowly discontinuous medially, and expanded and confluent ventrally), tegulae, mesoscutum with spot on disc and horizontal mark above fore wing, central and anterolateral spots on mesoscutellum, axillae, disc and anterolateral spot on metanotum, spot on metapleuron, lateral U-shaped mark on propodeum, anterior vertical mark and small mark and adjacent spot near mid coxa on mesopleura, margins of mesosternal lamellae, apex of fore coxae, mark on inner and outer margins of mid and hind coxae apically, ventral surfaces and dorsal mark apical mark on femora, lunulate lateral line on posterior margin of T1-6 and S2-5 contiguous medially on tergites; orange colouration as follows: legs (except coxae, apex of fore trochanters, mid and hind trochanters, ventral surfaces and dorsal mark apical mark on femora). Margin of tegulae semitransparent. Wing membranes hyaline with veins orange to brown. Setae white.

Distribution. Only known from a single specimen from Rimbija I., Wessel Islands off the coast of Arnhem Land, Northern Territory.

Remarks. This species is distinguished from other species of *Caetrazygnus* by the apically truncate parameres and the straight lateral margins of the basiparameres. It also differs from *C. greggi* which has the base of the cuspis rounded rather than sinusoidal in profile and from *C. galbinus* which has more extensive

yellow colouration such that the sclerites are more yellow than black including a yellow spot on the prosterna and the yellow U-shaped lateral marks on the propodeum fused medially. This species is also distinguished by the punctures on the pronotum being most distinct posterolaterally and ventrally, and the fore coxae which are slightly convex.

This species is similar in colouration to *C. greggi*.

Etymology. The species name is derived from the type locality.

***Nitidothynnus* gen. nov.**

Type species. Here designated *Nitidothynnus purdiei* sp. nov.

Generic diagnosis. *Male.* Head, mesosoma and metasoma (especially dorsally) strongly polished and mostly obscurely punctate (such that punctures are sparse, and very small and shallow giving the appearance of the integument being impunctate especially on the vertex and pronotum). Clypeus convex basomedially, not carinate, narrowly truncate. Antennal prominence double U-shaped, medially sulcate, above plane of clypeus. Antennae long, longer than combined length of head and mesosoma, flagellar (except basal) segments four times longer than wide, apical six segments weakly arcuate. Maxillary palps with apical 3 segments each longer than basal 3 segments, fourth segment longest. Pronotum with lateral margins strongly convergent anteriorly, anterior margin raised but not carinate, anterior truncation transversely carinate ventrally and produced laterally such that the pronotum is produced anterolaterally. Mesopleura with longitudinal median groove ventrally. Fore trochanters long and strongly narrowed over most of length from base. Metasoma elongate-fusiform, sclerites weakly sclerotized (except S1 and S8) and at most slightly constricted (although more so basally on S3-5 and especially S2 and T2). T7 convex, becoming slightly produced and membranous apically, not carinate. S8 with lateral margins curved, trispinose with medial spine longest. Genitalia with basal ring of medium length, subcylindrical and (in profile) slightly curved; basiparameres subovate (viewed dorsally) and emarginate medially, apices of individual basiparameres produced and often acute; parameres long and narrow especially apically, curved and convergent apically. All species are extensively marked with yellow on a reddish orange background although most of the reddish orange is replaced with black on the meso- and metathorax in some specimens.

Female. Mandible unidentate. Clypeus narrowly truncate to slightly emarginate, medially raised. Frons obscurely sagittally sulcate. Pronotum wider than long, anterior margin clearly defined, longer than posterior margin, anterolateral angles spinose, lateral margins carinate on posterior half ending in a small tooth anteriorly; disc slightly medially raised, raised area wider

posteriorly. Mesoscutellum narrow. Mesopleura with slight dorsal surface. Propodeum projecting well above level of mesoscutellum, oblique posteriorly becoming flattened dorsally, apex directed anteriorly and narrowed. Fore femur concave on apical half of ventral surface. T1 vertically truncate and setose anteriorly; dorsal surface with carinate apical margin and curved impressed preapical line. T2 impunctate with three to five transverse carinae. T3-5 with impressed curved preapical line. Pygidium (T6) curved in profile, posterior surface long and narrow with carinate lateral margins, ventral margins narrowly rounded, slightly emarginate laterally. Sternites sparsely and shallowly punctate.

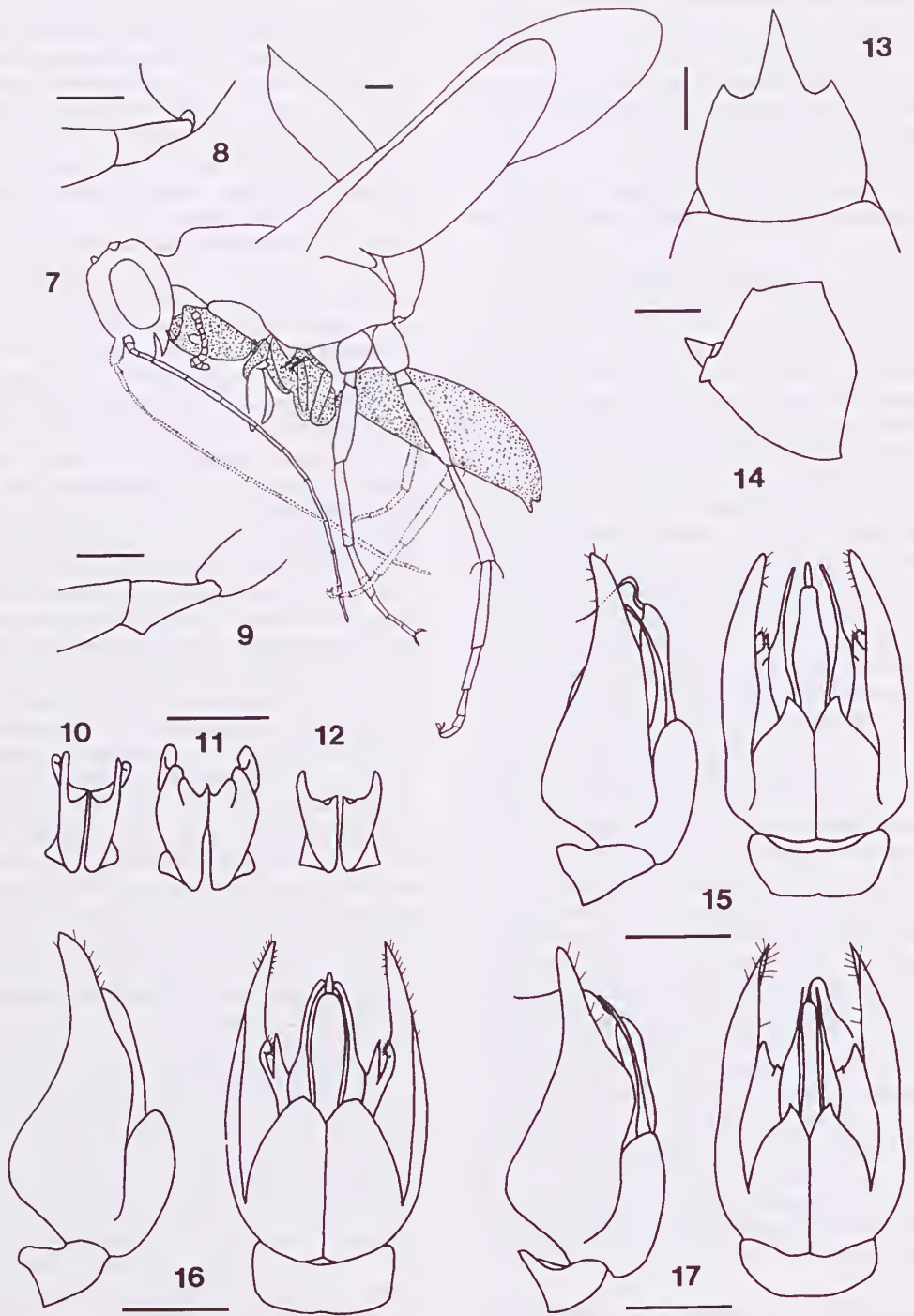
Remarks. The genus *Nitidothynnus* is most readily distinguished from other genera of the generic cluster by the microsculpture of the head, mesosoma and metasoma which are distinctively polished and obscurely punctate (particularly diagnostic on the vertex and pronotum); the anterior truncated surface of the pronotum transversely carinate ventrally and produced laterally and visible laterally as a short truncated process; the antennae relatively long; and the fore trochanters long and strongly narrowed over most of their length from the base. A convex, non-carinate clypeus that is below the plane of the antennal prominence, and long apical maxillary palp segments are similar to these states in *Neozeleboria*. However, *Neozeleboria* has S8 subparallel to subtriangular with the apex ranging from rounded to slightly emarginate but with only a single apical spine rather than with lateral margins curved with the apex trispinose.

Antennae are characteristically long in *Nitidothynnus* with antennae longer than the combined length of the head and mesosoma, and most flagellar segments four times longer than wide. In most other genera of the generic cluster (except some species of *Tachynomia* and closely related genera) they are shorter but distinctly longer than wide. This compares to the short antennae found in *Procerothynnus* in which the antennal segments are only slightly longer than wide, appearing virtually as long as wide.

The three species placed in this genus are very similar in appearance and are also best separated by the male genitalia, although *Nitidothynnus spinulus* is distinguished by the presence of a preapical spine on the fore and hind trochanters. Only the females of *N. purdiei* and *N. spinulus* are known, and these are distinguished by the shape of the head and T6. Both species are widespread in the Top End of the Northern Territory, and have overlapping distributions, while *N. ebeneus* is only known from the holotype from north-eastern Queensland.

Nitidothynnus was referred to as genus "B" by Brown (1998a) in a key to closely related genera.

Etymology. The generic name is masculine and is derived from the Latin word *nitidus* (= shining), and is a reference to the shining head, mesosoma and metasoma of the male.



Figs 7-17. *Nitidothynnus* spp., males: 7, *N. spinulus* sp. nov., male carrying female (female except eye and antenna stippled); 8, *N. purdiei* sp. nov., fore trochanter; 9, *N. spinulus* sp. nov., fore trochanter; 10, *N. purdiei* sp. nov., cuspis, ventral; 11, *N. spinulus* sp. nov., cuspis, ventral; 12, *N. ebeneus* sp. nov., cuspis, ventral; 13, *N. spinulus* sp. nov., S8; 14, *N. spinulus* sp. nov., prothorax lateral; 15, *N. spinulus* sp. nov., genitalia, lateral and dorsal; 16, *N. purdiei* sp. nov., genitalia, lateral and dorsal; 17, *N. ebeneus* sp. nov., genitalia, lateral and dorsal. Scale lines = 0.25 mm.

Key to species of *Nitidothynnus*. (The female of *N. ebeneus* is unknown)

1. a Male (winged) 2
b Female (wingless) 4
2. a Fore and hind trochanters with preapical spine on ventral margin (most conspicuous if viewed posteriorly) (Fig. 9) *N. spinulus* sp. nov.
b Trochanters without preapical spine on ventral margin (Fig. 8) 3
3. a Genitalia (viewed dorsally) with each basiparamere with outer margin curved and ending in an obtuse point (Fig. 16) and cuspis (Fig. 10) with ventral surface mostly horizontal becoming abruptly and strongly concave apically (excluding lamellate projection) *N. purdiei* sp. nov.
b Genitalia (viewed dorsally) with each basiparamere with outer margin sinusoidal and ending in an acute point (Fig. 17) and cuspis (Fig. 12) with ventral surface almost flat and sloping upwards towards apex, not abruptly truncated or concave apically (excluding lamellate projection) *N. ebeneus* sp. nov.
4. a Head with posterolateral angles emarginate (Fig. 20); T6 subparallel dorsally (Fig. 23) *N. spinulus* sp. nov.
b Head with posterolateral angles rounded (Fig. 21); T6 broadened ventroapically (Fig. 22) *N. purdiei* sp. nov.

***Nitidothynnus purdiei* sp. nov.**

(Figs 8, 10, 16, 21-22)

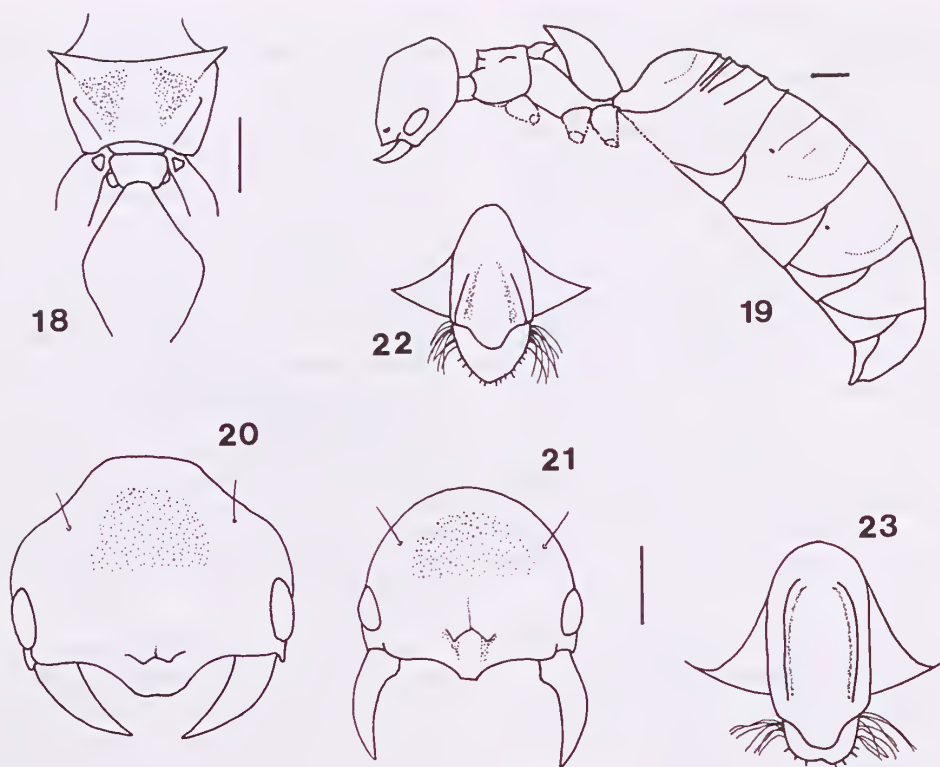
Type material. HOLOTYPE♂ - NTM (1912): near Oenpelli reservoir, campsite, 12°23'S, 133°05'E, 27 November 1997, G.R. Brown and J.E. Purdie. PARATYPES - *Northern Territory*: NTM (1913-1916) (4♂), same data as holotype; NTM (1917) (1♂), below Oenpelli reservoir, 12°24'S, 133°05'E, 27 November 1996, G.R. Brown and J.E. Purdie; NTM (1918) (1♂), near Oenpelli reservoir, by sweeping, 12°22'S, 133°04'E, 27 November 1996, G.R. Brown and J.E. Purdie; BMNH (E2000-27), QM (57840), NTM (1919-1920) (4♂), near Oenpelli, *Allosyncarpia* forest, 12°23'S, 133°01'E, 28 November 1996, G.R. Brown and J.E. Purdie; NTM (1921) (1♂), near Oenpelli, *Allosyncarpia* forest track, 12°23'S, 133°02'E, 30 November 1996, G.R. Brown and J.E. Purdie; NTM (1922) (1♂), Oenpelli reservoir, 12°24'S, 133°05'E, 26 November 1997, G.R. Brown and J.E. Purdie; NTM (1923-1924) (2♂), Daly River rd, Adelaide R. crossing, 13°29'S, 131°06'E, 24 October 1996, G.R. Brown; NTM (1925-1926) (2♂), Blackfellow Ck, Daly River rd, 13°32'S, 130°49'E, 19 November 1997, G.R. Brown; NTM (1927) (1♂), Groote Eylandt, in pit fall trap in open forest, 17-23 June 1982, J. Majer; NTM (1928) (1♂), near Drovers Rest, Litchfield NP, 25 November 1993, G.R. Brown; NTM (1929) (1♂), Maningrida, rubbish tip rd, 12°06'S, 134°13'E, 13 June

1996, G.R. Brown; NTM (1930) (1♂), Mataranka, by sweeping, 1 January 1996, G.R. Brown; NTM (1931) (1♂), 18°37'S, 137°59'E, Border Waterhole near Musselbrook Reserve, 10-17 April 1995, G.R. Brown; NTM (1932) (1♂), UDP Falls, 18-19 July 1980, M.B. Malipatil. NTM (11166) (1♀) Virginia near Darwin, 12°33'S, 131°02'E, 28 October 1996, S.M. Gregg (mounted with male paratype of *N. spinulus*). *Queensland*: NTM 1933-1937 (5♂), Musselbrook Reserve near Musselbrook Ck, 18°33'S, 138°11'E, 18 April 1995, G.R. Brown; ANIC (1♂), Holts Ck, 18°33'S, 138.11'E, 15 May 1995, at light, I.D. Naumann.

Other material. *Northern Territory*: NTM (2♂), near Oenpelli reservoir, by sweeping, 12°22'S, 133°04'E, 27 November 1996, G.R. Brown and J.E. Purdie; NTM (9♂), near Oenpelli reservoir, *Allosyncarpia* forest, 12°23'S, 133°02'E, 28 November 1996, 30 November 1996, G.R. Brown and J.E. Purdie; NTM (1♂), Oenpelli area, November 1996, G.R. Brown and J.E. Purdie. *Queensland*: NTM (4♂), Musselbrook Reserve near Musselbrook Ck, 18°33'S, 138°11'E, 18 April 1995, G.R. Brown.

Description of male. Body length 4.5-8 mm; fore wing 4-7 mm; hind wing 2.5-4 mm. Clypeus shallowly and closely punctate, apical margin width to maximum width 1:4.3. POL:OOL 1:1.6. Frons, vertex, gena and pronotum obscurely sparsely punctate. Lateral margins of pronotum slightly curved and convergent anteriorly, anterior truncation with ventral transverse carina almost continuous medially. Mesoscutum closely punctate anteriorly and laterally, punctures more conspicuous than those on head and pronotum. Mesoscutellum and metanotum obscurely sparsely punctate. Propodeum transversely striate, longer than wide, lateral margins parallel-sided anteriorly, dorsal margin in profile evenly rounded down to metasoma. Mesopleura obscurely sparsely punctate. Fore coxae, long, conical, ventral surface flat. Fore trochanter (Fig. 8) not spined. Metasoma almost impunctate, T1 closely punctate, T6-7 and S6-8 with conspicuous setiferous punctures and setae long. T1 width to length 1:1.1. S1 medially raised, rounded in cross-section, T2 weakly and S2 strongly depressed anteriorly, segments 1-5 flattened and wider than high. Genitalia as in Figure 16: apex of each basiparamere rounded dorsoapically; parameres narrow and narrowly subtriangular; cuspis (Fig. 10) lamellate apically, ventral surface mostly horizontal becoming abruptly and strongly concave apically (excluding lamellate projection).

Colour. Reddish orange; yellow colouration as follows: mandibles (except apex), maxillary and labial palps, clypeus (except medial anchor-shaped mark and dorsolateral spots testaceous), antennal prominence, inner orbits of eyes extending to behind vertex, outer orbits sinusoidally extending across vertex and confluent with inner orbits, margins of pronotum (broadly so



Figs 18-23. *Nitidothynnus* spp., females: 18, *N. spinulus* sp. nov., mesothorax; 19, *N. spinulus* sp. nov., habitus; 20, *N. spinulus* sp. nov., head; 21, *N. purdiei* sp. nov., head; 22, *N. purdiei* sp. nov., T6; 23, *N. spinulus* sp. nov., T6. Scale lines = 0.25 mm.

ventrally), tegulae, mesoscutum with curved mark above fore wing and central subrectangular marks, mesoscutellum with anterolateral spot and central broad trident-shaped mark; disc and anterolateral line on metanotum, most of propodeum, mesopleuron (except curved branched medial mark and ventral surface), metapleuron (except extreme margins), coxae (except extreme bases), margins of mesosternal lamellae, apical margins of trochanters and inner surface of fore trochanter, dorsal and ventral margins of femora irregularly expanded on fore leg, outer surface of tibiae, lateral irregular spots on T1-6 and S1-2; black colouration as follows: ocellar triangle, posterior and posteroventral surfaces of head, anterior truncation and neck of pronotum, mesoscutum (except curved mark above fore wing and central subrectangular marks), mesoscutellum laterally and extreme anterior margin, metanotum (except disc and anterolateral line), extreme anterior margin of and pair of posteromedial spots on propodeum, prosterna, mesopleuron ventrally, extreme margins of metapleuron, S1, S8 and base of T1; tarsi brown especially apically. Wing membranes hyaline, veins orangish brown.

Description of female. Body length 3 mm. Head (Fig. 21) rounded, as wide as long, sparsely punctate with large

semicircular closely punctate area occupying most of vertex, posterolateral angles strongly emarginate. T2 with 3 transverse carinae, apical 2 strongest, basal 1 may be obscured by T1. Pygidium (T6) with lateral margins slightly diverging ventrally, and slightly medially and triangularly raised (Fig. 22).

Colour. Pale yellowish brown; head (except appendages) greyer.

Distribution. Northern Territory from Daly River south to Mataranka and east to the Queensland border.

Remarks. The male of this species is distinguished from other species of *Nitidothynnus* by the structure of the genitalia which (when viewed dorsally) has each basiparamere with the outer margin curved and ending in an obtuse point (Fig. 16) and cuspis (Fig. 10) with the ventral surface mostly horizontal becoming abruptly and strongly concave apically. The female is distinguished by the structure of the head which has the posterolateral angles rounded (Fig. 21) and T6 broadened ventro-apically (Fig. 22). The only other known female of a species in the genus *Nitidothynnus* has the posterolateral angles of the head emarginate (Fig. 20) and T6 subparallel dorsally (Fig. 23).

The yellow markings may be expanded on the posterior and anterior margins of the pronotum so that

they are confluent each side of the sagittal line, or confluent medially on S1. They may also be narrowly discontinuous medially on the anterior margin of the pronotum, reduced to a central spot on the pronotum or split into 2 spots on the mesopleuron and replaced with reddish orange, or reduced or absent on S1-2 and T1. Much of the reddish orange on the mesoscutum and propodeum may be replaced with black. The apex of the metasoma may be slightly darker.

The Musselbrook Reserve specimens tend to have the mesosoma darker than the majority of the other specimens, but fit within the range of colour variation of these specimens. There are no noticeable differences in the genitalia to justify a separate species for the Musselbrook material.

The specimen from Groot Eylandt is labelled as coming from a pit fall trap. This is unusual, but it is conceivable that a wingless female could have fallen into such a trap, and, once there, attracted the male by pheromones. I have never seen thynnines of either sex in pit fall traps, although the wingless females of the closely related family Mutillidae ("velvet ants") are frequently caught in such traps.

Etymology. This species is named after John Purdie who collected many of the type series, and who is a keen naturalist and a close friend.

Mating biology. As indicated in the Introduction, mixed species pairs may be encountered occasionally. This is indicated in museum collections when a series consisting of a single species of male includes females of two different species that have both been collected in copula with this species of male. In the absence of morphological structures that may, for example, be adaptations to prolonged coupling, and therefore, associate pairs, sexes may be associated on the assumption that the majority of specimens couple correctly. This is the case with *Nitidothynnus purdiei* and *N. spinulus*.

Females of *Nitidothynnus purdiei* and *N. spinulus* are associated with males on the basis of coincident collecting data for four males and one female of *N. spinulus* from Virginia, and two males and two females *N. spinulus* from Berrimah. The Virginia specimens include a pair collected in copula while the Berrimah females include a pair grasping each other and which had probably been in copula prior to being killed.

The Berrimah pair is interesting in the way the male and female fit closely together. The male is clasping the female with its legs such that: the hind trochanteral spine fits into the groove before the apical carina on T2 of the female; the fore trochanteral spine is holding the fore femur of the female away from her body; and the male head is deflexed so that the female head is held closely between the mouthparts and the fore coxae of the male. The female is clasping the male with her mouthparts and has the fore femur overlapping the fore trochanter and

femur of the male, and has the protruding propodeum slotted into the longitudinal ventral groove along suture of the mesopleura of the male.

Contrary to this association of sexes is another female in which the head is rounded posterolaterally and T6 is broadened ventrally. This female was collected in copula at Virginia with a male of *N. spinulus*. The female is believed to be *N. purdiei* as it is the only other species which overlaps in distribution with *N. spinulus* (although there are no other coincident collecting records).

As pairs couple for prolonged periods, there is the possibility that the shape of structures in the two sexes that are juxtaposed as a result of this coupling, may be correlated. The major differences in the shape of the female head, and the juxtaposition of the female head and male fore coxae in Figure 7 suggests that there may be a correlation between these structures that permit the association of sexes on morphological grounds. However, no differences in the structure of the male fore coxae could be found that would explain differences in the female head shape.

Nitidothynnus ebenus sp. nov.

(Figs 12, 17)

Type material. HOLOTYPE ♂ - QM (T57841): near Granite Gorge, 17°01'S. 145°20'E, 21 May 1989, 12 km SW Mareeba, Queensland, G. and A. Daniels.

Description of male. Body length 7 mm; fore wing 5 mm; hind wing 4 mm. Clypeus with apical margin width to maximum width 1:5.0. POL:OOL 1:1.5. Anterior truncation of pronotum with ventral transverse carina broadly discontinuous medially. Fore trochanter not spined. T1 width to length 1:1.2. Genitalia as in Figure 17: apex of each basiparamere narrow and acute dorsoapically; parameres subtriangular, strongly narrowed beyond level of apex of cuspis; cuspis (Fig. 12) lamellate apically, ventral surface almost flat and sloping upwards towards apex, not abruptly truncated or concave apically (excluding lamellate projection). Otherwise as *N. purdiei*.

Colour. Black; yellow colouration as follows: mandibles (except apex), maxillary and labial palps, clypeus (except testaceous medial anchor-shaped), antennal prominence, inner orbits of eyes extending to behind vertex, outer orbits of eyes sinusoidally extending across vertex and confluent with inner orbits, anterior and posterior margins of pronotum, tegulae, mesoscutum with curved mark above fore wing and central sub-rectangular marks, mesoscutellum with anterolateral spot and central broad inverted T-shaped mark, disc and anterolateral line on metanotum, propodeum with medial line strongly broadened anteriorly and lateral line strongly broadened posteriorly, mesopleuron (except curved branched medial mark and ventral surface), spot on metapleuron, fore and mid coxae (except extreme bases), outer margin of hind coxa, margins of mesosternal

lamellae, apical margins of trochanters, dorsal and ventral margins of femora, outer surface of tibiae, lateral irregular spots on T1-5; reddish orange colouration as follows: gena and vertex dorsally, legs (except coxa and yellow marks on trochanters, femora, tibiae and tarsi) and metasoma (except yellow spots on T1-5, T1, S1, base of S2 and S8); S8 dark brown. Wing membranes hyaline, veins pale orange.

Distribution. Known only from near Granite Gorge, 12 km SW of Mareeba, North Queensland.

Remarks. The male of this species is readily distinguishable from other species of the genus by the absence of reddish orange colouration on the mesosoma (excluding the legs) although this is based only on a single specimen. It is also distinguished by the digiti which are not visible ventrally and the cuspis (Fig. 12) which has the ventral surface almost flat and sloping upwards towards apex, not abruptly truncated or concave apically. The female is unknown.

Etymology. The species name is derived from the Latin word *ebeneus* (= black) and refers to the relatively dark colour of the mesosoma.

Nitidothynnus spinulus sp. nov.

(Figs 7, 9, 11, 13-15, 18-20, 23)

Type material. HOLOTYPE ♂ - NTM (1954): Virginia near Darwin, 12°33'S, 131°02'E, Northern Territory, 28 October 1996 S.M. Gregg. PARATYPES - *Northern Territory*: NTM (1955-1958) (3♂, 1♀), same data as holotype (1♂, 1♀ 1955-1956), or dated 12 July 1997 (1♂ 1957) or 16 November 1997 (1♂ 1958); NTM, (1959-1962) (2♂, 2♀), Berrimah near Darwin, 1-15 November 1996 (1♂ 1959), 16-30 November 1996 (1♂, 2♀ 1960-1962), A. Salvarani; NTM (1963-1965), OTTAWA, WAM (26556) (5♂), Darwin, eucalypt woodland, Malaise trap, (site 93-86), 1-25 December 1993, S. and J. Peck; NTM (1966-1967), QM (T57842) (3♂), Anbangbang Billabong, Kakadu NP, 12°52'S, 132°48'S, 10 June 1996 (1 NTM 1966), 17 January 1998 (1 NTM 1967), 1 QM), G.R. Brown; ANIC, NTM (1968-1973), OTTAWA (8♂), Kapalga Research Stn, Kakadu NP, eucalypt woodland, Malaise trap, (site 93-117), 11-25 December 1993, S. and J. Peck; NTM (1974-1975), OTTAWA (3♂), Kapalga Research Stn, Kakadu NP, North Point Rainforest, Malaise trap, (93-134), 24 December 1993-7 January 1994, S. and J. Peck; NTM (1976) (1♂), Keep River National Park, Gurrandalng, 15°53'S, 129°03'E, 30 April 1996, G.R. Brown; NTM (1977) (1♂), Keep River National Park, Gurrandalng, 15°53'S, 129°03'E, 29 April 1996, G.R. Brown.

Other material. NTM (1♂), Keep River National Park, Gurrandalng, 15°53'S, 129°03'E, 29 April 1996, G.R. Brown.

Description of male. Body length 5-7 mm; fore wing 4-6 mm; hind wing 3-4 mm. Clypeus with apical margin width to maximum width 1:4.8. Anterior truncation of

pronotum with ventral transverse carina broadly discontinuous medially. Fore and hind trochanters with ventral preapical spine. Genitalia as in Figure 15: apex of each basiparamere acute dorsoapically; parameres narrow and narrowly subtriangular; cuspis (Fig. 11) lamellate apically, ventral surface oblique. Otherwise as *N. purdiei*.

Colour. Similar to *Nitidothynnus purdiei* except that at most S2 has a pair of pale spots, the apex of S1 is reddish orange, and the basal three tarsomeres are yellowish ventrally and brown dorsally with the apical two tarsomeres uniformly dark brown.

Description of female. Body length 4 mm. Head (Fig. 20) rounded, slightly wider than long, sparsely punctate with semicircular closely punctate area on vertex, posterolateral angles strongly emarginate. T2 with 5 transverse carinae, apical 3 strongest, basal 2 may be obscured by T1. T3-5 with impressed curved preapical line preceded by a curved line of punctures. Pygidium (T6) with lateral margins parallel (Fig. 23).

Colour. Orangish-brown; coxae, trochanters, femora and mesosoma (except prothorax) slightly darker; tibiae and tarsi slightly paler.

Distribution. Top End of Northern Territory between Darwin and Kakadu National Park.

Remarks. This species is distinguished from all other species of *Nitidothynnus* by the presence of a preapical spine (most reliably viewed on the posterior surface) on the ventral margin of the fore and hind trochanters of the male. The female is distinguished by the structure of the head which has the posterolateral angles emarginate (Fig. 20) and T6 which is subparallel dorsally (Fig. 23). The only other known female in the genus, *N. purdiei*, has the posterolateral angles of the head rounded (Fig. 21) and T6 broadened ventroapically (Fig. 22).

Etymology. The species name is derived from the Latin word for a spine, and refers to the preapical spine on the fore and hind trochanters.

Procerothynnus gen. nov.

Type species. Here designated *Procerothynnus centralianus* sp. nov.

Generic diagnosis. *Male.* Head, mesosoma and metasoma polished. Clypeus closely and finely punctate, sagittally carinate, narrowly produced, convex medially, convexity extending medially almost to apical margin of clypeus. Antennal prominence V-shaped, sagittally sulcate, not carinate, not strongly raised, at level of clypeus. Antenna very short, not reaching back to propodeum, flagellar segments only slightly longer than wide, apical six segments slightly arcuate. Maxillary palp segments 2-6 subequal, segments 4 and 6 slightly longer. Pronotum with lateral margins curved and convergent anteriorly, anterior margin sharply raised and subcarinate. Metasoma fusiform, segments 3-4 widest, segments wider than high. T2 depressed anteriorly, T3 at most

slightly depressed anteriorly. T7 convex becoming slightly produced and membranous apically, not carinate. S1 broadly medially raised. S8 rounded apically, without spines. Genitalia laterally compressed; basal ring short and predominantly membranous with narrow, sclerotized ring basally; basiparameres fusiform (viewed dorsally) with apical margin sinusoidal, strongly rounded (viewed laterally); paramere subtriangular to subquadrate; aedeagus long and narrow.

Remarks. *Procerothygnus* is distinguished from other genera of the generic cluster (and all other Australian Thynninae) by the combination of a medially convex clypeus that is sagittally carinate; very short antennae which do not reach back to the propodeum; S8 apically rounded and without spines; and the genitalia laterally compressed. A convex clypeus with a sagittal carina and S8 that is not apically spinose suggest a relationship with *Zelexoria*, *Psammothynnus* and *Chilothynnus*. However, the former two have the clypeus strongly convex and broadly produced and apically truncate. *Psammothynnus* also has S8 apically emarginate. *Chilothynnus* is the closest genus, but differs by having lateral spines on S8 (Brown 1997a), and together with all other Thynninae lack very short antennae and laterally compressed genitalia as found in *Procerothygnus*.

The three species placed in this genus are similar in appearance and are most reliably identified from the male genitalia. However, head colour appears reliable in distinguishing *P. arnhemicus* sp. nov. from other species of *Procerothygnus*. All are known from relatively few specimens from relatively few locations: *P. centralianus* sp. nov. from four locations in the East MacDonnell Ranges in central Australia; *P. arnhemicus* sp. nov. from near Oenpelli in western Arnhemland and *P. carpentarianus* sp. nov. from Musselbrook Reserve near the Northern Territory border in north-western Queensland. Like *Nitidothynnus*, nothing is known about the biology of *Procerothygnus*. All specimens were collected from habitats with loamy or sandy soil and near water courses (although all except the stream at Oenpelli, but including the stream at Musselbrook Reserve, were dry at the time at which specimens were collected).

Etymology. The generic name is masculine and is derived from the Latin word *procerus* which means tall and slender, and is a reference to the shape of the male genitalia which are relatively high (in profile) and slender (viewed dorsally).

Key to males of *Procerothygnus*. (Females are unknown.)

1. a Yellow marks above each antennal insertion at least partially confluent medially; mesoscutum above fore wing with at most a small yellow spot; genitalia with parameres broad and apex of basiparameres weakly sinusoidal (Figs 27, 29)
..... *P. arnhemicus* sp. nov.

- b Antennal prominence with separate and discrete spot above each antennal insertion; mesoscutum with a longitudinal mark above fore wing; genitalia with parameres subtriangular and apex of basiparameres emarginate (Figs 25-7, 28) 2
2. a Punctures on propodeum relatively deep, discrete and distinct; genitalia as in Figure 25; apical margin of basiparameres weakly sinusoidal, slightly produced medially and apicolaterally
..... *P. centralianus* sp. nov.
- b Punctures on propodeum shallow, often not discrete; genitalia as in Figures 26; apical margin of basiparameres (Fig. 28) strongly emarginate, produced medially and strongly produced apicolaterally *P. carpentarianus* sp. nov.

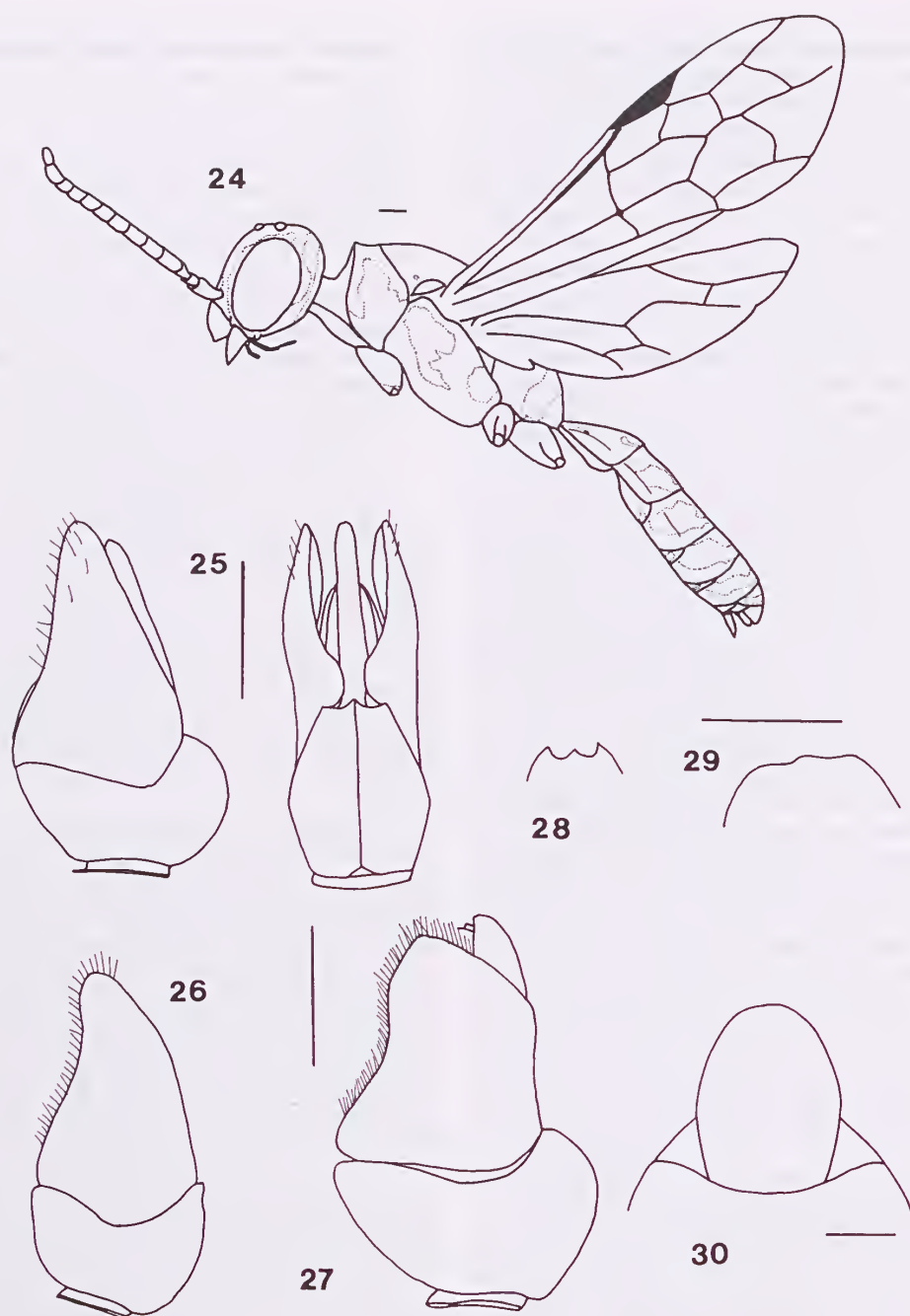
***Procerothygnus centralianus* sp. nov.**

(Figs 25, 30)

Type material. HOLOTYPE ♂ - NTM (1979): near Ghost Gum, 23°32'S, 134°23'E, Trephina Gorge Nature Park, Northern Territory, 26 February 1997, G.R. Brown. PARATYPES - Northern Territory: NTM (1980) (1♂), Ross River Highway 23°38'S, 134°18'E, 6.2 km W of Trephina Gorge Nature Park, 1 March 1997, G.R. Brown; NTM (1981) (1♂), road to Ruby Gap Nature Park, 23°29'S, 134°54'E, 2 March 1997, G.R. Brown; NTM (1982) (1♂), Corroboree Rock Conservation Reserve, 23°41'S, 134°13'E, 1 March 1997, G.R. Brown.

Description of male. Body length 6.5-7 mm; fore wing 5-6 mm; hind wing 4-5 mm. Frons shallowly punctate to shallowly closely punctate, punctures becoming aligned longitudinally on antennal prominence. Clypeus with apical margin width to maximum width 1:4.2. POL:OOL 1:0.9. Vertex and gena shallowly rugosely punctate. Pronotum closely punctate. Mesoscutum punctate to sparsely punctate, closely punctate near anterior margin. Mesoscutellum and metanotum sparsely punctate. Propodeum closely to rugosely punctate, punctures discrete. Mesopleuron closely to rugosely punctate becoming punctate ventrally. Fore coxae with ventral surface almost flat, subparallel basally, subtriangular apically. T1 width to length 1:1.0. Tergites almost impunctate, punctures shallow, transverse and slit-like on most segments, deeper and rounder on T6-7. T3 not depressed anteriorly. Sternites almost impunctate but with punctures aligned in transverse straight or curved lines, S8 closely punctate. Genitalia as in Figure 25; apical margin of basiparameres weakly sinusoidal, slightly produced medially and apicolaterally.

Colour. Black; yellow colouration as follows: clypeus (except medial anchor-shaped mark), mandibles (except apex), large spot above each antennal insertion, inner orbits continuous across vertex, outer orbits, margins of pronotum broadly confluent medially (except small central spot), tegulae, mesoscutum with curved mark



Figs 24-30. *Procerothylnus* spp., males: **24**, *P. arthemius* sp. nov., habitus; **25**, *P. centralianus* sp. nov., genitalia, lateral and dorsal; **26**, *P. carpentarianus* sp. nov., genitalia, lateral; **27**, *P. arthemius* sp. nov., genitalia, lateral; **28**, *P. carpentarianus* sp. nov., apical margin of basiparameres; **29**, *P. arthemius* sp. nov., apical margin of basiparameres; **30**, *P. centralianus* sp. nov., S8. Scale lines = 0.25 mm.

above fore wing and large medial subrectangular mark, mesoscutellum with large medial mark and smaller anterolateral spot, metanotum with disc, posterior margin narrowly and mark on anterior margin, metapleuron with large medial spot, broad sinusoidal transverse band on propodeum, three dorsal spots on mesopleuron, anterior spot largest, posterior spot near mid coxa smallest, coxae (except basally), apices of femora extending along ventral margin to base and along dorsal margin apically especially on fore leg, line on outer surface of tibiae, margins of mesosternal lamellae, lateral spot on T1-6 and S2-5 (smaller or inconspicuous on sternites) extending medially as a curved line near posterior margin of sclerites, posteromedial spot on S1; orange colouration as follows: apex of mandibles, lateral parts of anchor-shaped mark on clypeus, legs (except coxae and yellow marks); much of T1 apically, T2-3 and S2-3, reddish orange. Wing membranes hyaline, veins pale orange to brown.

Distribution. Eastern MacDonnell Ranges, Northern Territory.

Remarks. This species is distinguished from other species of *Procerothynnus* by the presence of relatively shallow punctures on the frons, a weakly developed clypeal carina, and the genitalia (Fig. 25) which have the apical margin of basiparameres weakly sinusoidal and slightly produced medially and apicolaterally.

Yellow colouration may be reduced such that marks and spots are smaller on some sclerites. In particular this colouration may be limited on the clypeus to the apical margin laterally, on the pronotum to the margins only, on the propodeum as lateral spots, on the tergites and sternites as a curved lateral line without a large lateral spot, and reduced on the legs especially the femora. The reddish orange colouration on the metasoma may be replaced with black as may some of the orange colouration on the legs. The Ruby Gap specimen is much darker than the other specimens but there is no noticeable difference in the genitalia.

Etymology. This specific name refers to the central Australian distribution of this species. It is intended to be construed as adjectival.

Procerothynnus arnheimicus sp. nov.

(Figs 24, 27, 29)

Type material. HOLOTYPE ♂ - NTM (1983): campsite near Oenpelli Reservoir, 12°23'S, 133°05'E, Oenpelli, Northern Territory, 27 November 1997, G.R. Brown and J.E. Purdie. PARATYPES - *Northern Territory*: ANIC, NTM (1984) (2♂), data as holotype; BMNH (E2000-27), NTM (1985-1986), WAM (26557) (3♂), Leaning Tree Lagoon, 12°43'S, 131°25'E, 11 December 1997, G.R. Brown and J.E. Purdie.

Other material. NTM (1♂), Leaning Tree Lagoon, 12°43'S, 131°25'E, 11 December 1997, G.R. Brown and J.E. Purdie.

Description of male. Body length 6 mm; fore wing 4.5 mm; hind wing 3.5 mm. Frons closely to rugosely punctate. Clypeus with apical margin width to maximum width 1:4.3. POL:OOL 1:1.2. Vertex and gena shallowly rugosely punctate, punctures more discrete on gena. Pronotum closely punctate becoming impunctate ventrally. Mesoscutum punctate, punctures sparser medially. Mesoscutellum and metanotum sparsely punctate. Propodeum closely to rugosely punctate, punctures discrete. Mesopleuron closely to rugosely punctate becoming sparsely punctate ventrally. Fore coxae with ventral surface convex, subtriangular. T1 width to length 1:1.0. Tergites almost impunctate, punctures shallow, transverse and slit-like on most segments, deeper and rounder on T7 although punctures sparser medially. T3 at most slightly depressed anteriorly. Sternites almost impunctate, closely punctate on S8. Genitalia as in Figure 27; apical margin of basiparameres (Fig. 29) weakly sinusoidal, not produced apically.

Colour. As in *P. centralianus* except spots above antennal insertions partially confluent medially, mark above fore wing reduced to a small inconspicuous spot or absent, middle spot on mesopleuron small and posterior post absent, marks on most metasomal segments strongly curved, and metasoma without reddish orange colouration. Wing veins generally paler except subcosta.

Distribution. Known only from the vicinity of Kakadu National Park, Northern Territory.

Remarks. This species is readily distinguished from other species of *Procerothynnus* by having separate yellow spots above each antennal insertion, at most a small yellow spot on the mesoscutum immediately above the base of the fore wing, and the structure of the genitalia (Fig. 27), which have the apical margin of basiparameres (Fig. 29) weakly sinusoidal and not produced apically.

Etymology. This specific name is derived from the type locality. It is intended to be construed as adjectival.

Procerothynnus carpentarianus sp. nov.

(Figs 26, 28)

Type material. HOLOTYPE ♂ - UQIC: Murrays Spring, 18°35'15"S, 138°04'28"E, 7km W of Musselbrook Resource Center, Lawn Hill National Park, Queensland, 200 m, 10 May 1995, G. Daniels, M.A. Schneider. PARATYPES - *Queensland*: UQIC (1♂), data as holotype dated 4 May 1995.

Description of male. Body length 6 mm; fore wing 4.5 mm; hind wing 3.5 mm. Frons shallowly rugosely punctate. Clypeus with apical margin width to maximum width 1:4.0. POL:OOL 1:1.2. Vertex and gena shallowly punctate. Pronotum punctate becoming longitudinally rugulose ventrally. Mesoscutum punctate. Mesoscutellum and metanotum sparsely punctate.

Propodeum closely to rugosely punctate, punctures shallow and not always discrete. Mesopleuron punctate. Fore coxae with ventral surface almost flat, subtriangular. T1 width to length 1:1.5. Tergites almost impunctate, punctures shallow, transverse and slit-like on most segments, deeper and rounder on T6-7 although punctures sparser medially. T3 not depressed anteriorly. Sternites almost impunctate, S1 and S8 closely punctate. Genitalia as in Figure 26; apical margin of basiparameres (Fig. 28) strongly emarginate, produced medially and strongly produced apicolaterally.

Colour. As in *P. centralianus* except middle spot on mesopleuron small and posterior spot absent, yellow marks on sternites mostly absent, and metasomal segment 3 is darker with less reddish orange. Wing veins generally paler except subcosta.

Distribution. Known only from two specimens from Musselbrook Reserve north-western Queensland on the border of the Northern Territory.

Remarks. This species is easily distinguished from the other two species of the genus by shallower and less discrete punctures on propodeum, and the structure of the genitalia (Fig. 26), which have the apical margin of basiparameres strongly emarginate and produced medially and strongly produced apicolaterally (Fig. 28).

Etymology. This specific name is derived from The Gulf of Carpentaria which is the broader Australian region from which the types were collected. It is intended to be construed as adjectival.

ACKNOWLEDGMENTS

I thank Steven Gregg and John Purdie for their interest in entomology in general and tiphiids in particular, the curators of the above listed institutions for the loan of material in their care, and the anonymous referees for comments on an earlier version of this paper. I also thank Dr Richard C. Willan for his comments and eye for detail.

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A new bythitid genus and species, *Acarobythites larsonae*, from shallow rocky reefs off northern Australia (Pisces, Ophidiiformes, Bythitidae)

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ABSTRACT

A new genus and species of the subfamily Bythitinae (Bythitidae), *Acarobythites larsonae*, is described from two specimens, 25.2 mm and 18.6 mm standard length, collected from pools on rocky reefs in the Northern Territory, Australia. This genus resembles *Microbrotula* Gosline, 1953 in the counts of pectoral and pelvic fin rays, branchiostegal rays and developed rakers on the anterior arch, and in having a normal pectoral peduncle, lower angle of preopercle without spines, sharp-pointed jaw teeth and vomerine and palatine teeth. However, it is clearly distinguishable from the latter in the following characters: head and body scaleless, relatively small eyes (diameter 17.8-18.0 times in head length), snout compressed, posterior end of maxillary rounded and lacking a ventrally-directed process near its postero-ventral corner, opercular spine flat and weak, 11-12 caudal fin rays and 42-43 total vertebrae.

KEYWORDS: Ophidiiformes, Bythitidae, Australia, new genus, *Acarobythites*.

INTRODUCTION

Cohen and Nielsen (1978) included 15 genera in the subfamily Bythitinae of the viviparous fish family Bythitidae. This subfamily is characterised by having dorsal and anal fins continuous with the caudal fin, and is separable from the free-tailed Brosmophycinae, the other member of the family (Cohen and Nielsen 1978). Since Cohen and Nielsen (1978), only *Hastatobythites* Machida, 1977 has been added to the Bythitinae (Cohen and Nielsen 1999).

Recently, two small bythitid specimens were sent to the author for examination by Dr Helen K. Larson of the Museum and Art Gallery of the Northern Territory (NTM), Darwin, Australia. These specimens had dorsal and anal fins continuous with the caudal fin. Although they resembled the small-sized bythitine genus *Microbrotula* Gosline, 1953, known from Hawaii (Gosline 1953) and from Samoa and Vanuatu (Cohen and Wourms 1976), they were easily distinguishable from *Microbrotula* by the absence of scales on the head and body. The specimens are here described as a new genus and species.

Measurements and enumeration follow Machida (1993). Standard length and head length are expressed as SL and HL, respectively.

SYSTEMATICS

Family Bythitidae Gill, 1861

Subfamily Bythitinae Gill, 1861

Acarobythites new genus

Type species. *Acarobythites larsonae* new species, by monotypy.

Diagnosis. A genus of the subfamily Bythitinae (Cohen and Nielsen 1978: 42) with: head and body scaleless; anal fin origin at about mid-body; eye diameter 17.8-18.0 times in HL, snout compressed; posterior end of maxillary rounded, not sheathed by dermal cheek fold, without ventrally-directed process near postero-ventral corner; opercular spine flat and weak; no pore-bearing skin flap on upper angle of opercle; lower angle of preopercle smooth; pectoral peduncle normal, broader than long; no spine on eleuthrum; all teeth sharp-pointed, some needle-like; teeth present in jaws and on vomer and palatines; developed gill rakers on anterior arch 3; pectoral fin rays 13-14; pelvic fin ray 1; caudal fin rays 11-12; branchiostegal rays 7; 12-13 precaudal vertebrae, with sharp-pointed neural spines; and 42-43 total vertebrae.

Description. See species description below.

Remarks. According to Cohen and Nielsen (1972, 1978), Cohen (1987), and Machida (1997), the following genera in the subfamily Bythitinae are known to have

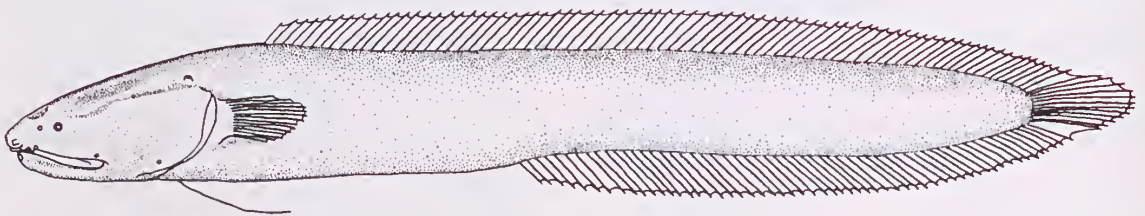
Table 1. Comparison between *Acarobythites* gen. nov. and *Microbrotula* Gosline, 1953. * = orbit diameter.

Genus (Source)	<i>Acarobythites</i> gen. nov. (this work)	<i>Microbrotula</i> Gosline, 1953 (Gosline 1953; Cohen and Wourms 1976; Cohen and Nielsen 1978)
Head squamation	scales absent	partly naked
Body squamation	scales absent	complete
Anal fin origin	at about mid-body	at about mid-body
Eye diameter	17.8-18.0 in HL	(6.4-15.4 in HL)*
Snout	compressed	depressed
Posterior end of maxillary	rounded, not sheathed, without ventrally-directed process	expanded, not sheathed, with ventrally-directed process
Pectoral peduncle	broadier than long	broadier than long
Opercular spine	flat and weak	sharp and needle-like
Lower angle of preopercle	smooth	smooth
Teeth	sharp-pointed	not all tiny and granular
Palatine teeth	present	present
Vomerine teeth	present	present
Developed rakers on anterior arch	3	3-4
Pectoral fin rays	13-14	10-14
Pelvic fin ray	1	1
Caudal fin rays	11-12	4-6
Branchiostegal rays	7	7
Precaudal vertebrae	12-13	11-13
Total vertebrae	42-43	51-56

seven branchiostegal rays: *Bythites* (7-8 rays), *Calamopteryx*, *Microbrotula*, *Saccogaster* (7-9 rays), *Stygnobrotula* and *Thalassobathia*. Although Cohen and Nielsen (1978) did not report the number of branchiostegal rays for *Bellotia*, this genus apparently differs from *Acarobythites* only in lacking pelvic fins. Among these genera having seven branchiostegal rays, two of them, *Calamopteryx* and *Saccogaster*, are well characterized by having an elongated pectoral peduncle (Cohen and Nielsen 1978). *Stygnobrotula* lacks palatine teeth, and *Thalassobathia* has two rays in each pelvic fin (Cohen and Nielsen 1978). *Bythites* has a scaleless head, completely scaled body, 24-30 pectoral fin rays, 0-1 developed gill rakers on the anterior arch, and the anal fin origin is positioned well behind the mid-body (Nielsen and Cohen 1973; Cohen and Nielsen 1978). Cohen and Wourms (1976) gave a revised diagnosis for

Microbrotula, when they described a new species, *M. randalli*. They regarded small eyes, less than six times in head length, as one of the diagnostic characteristics of *Microbrotula* (Cohen and Wourms 1976). Orbit diameter ranges from 6.4 to 8.4 times and from 11.0 to 15.4 times in head length in *M. randalli* and in *M. rubra*, respectively (Cohen and Wourms 1976). Table 1 compares *Acarobythites* and *Microbrotula*. *Acarobythites* appears to be distinguishable from the latter by its naked head and body, small eye, compressed snout, posterior end of maxillary rounded, no ventrally-directed process at the postero-ventral corner of maxillary, opercular spine flat and weak, and 11-12 caudal fin rays.

Etymology. The generic name is derived from the Latin, *acaro* (small), in reference to its small body, combined with *Bythites* (gender: masculine), one of the known genera in the family Bythitidae.

**Fig. 1.** *Acarobythites larsonae* sp. nov., NTM S.14665-026, holotype, 25.2 mm SL, from Australia. Scale bar indicates 5 mm.

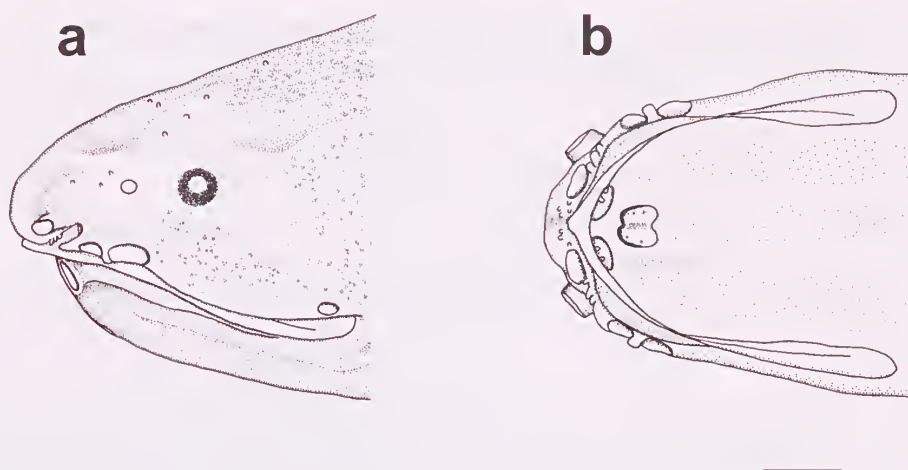


Fig. 2. Lateral (a) and ventral (b) views of anterior part of head of NTM S. 14665-026, holotype of *Acarobythites larsonae* sp. nov. Scale bar indicates 1 mm.

Acarobythites larsonae new species

(Figs 1-4)

Type material. HOLOTYPE - NTM S.14665-026, 25.2 mm SL, sex unknown, northwestern side of Field Island (12°04.20'S, 132°19.31'E), Northern Territory, Australia, rock pools on reef, depth 0.3 m, substrate sand, mud, oyster covered rocks, coll. R. Williams and party, 5 June 1998. PARATYPE - NTM S.10015-049, 18.6 mm SL, sex unknown, on silty sand with isolated coral clumps and rubble piles, off reef flat on E side of Coral Bay, Cobourg Peninsula, Northern Territory, depth 3-4 m, coll. H. K. Larson, 17 Oct. 1981.

Diagnosis. See generic diagnosis.

Description. Data on the holotype given first, data on the paratype in parentheses when differing from holotype.

Counts: dorsal fin rays 79 (73), anal fin rays 57 (53), caudal fin rays 12 (11), pectoral fin rays 14 (13), pelvic fin ray 1, branchiostegal rays 7, developed gill rakers on anterior arch 3, pseudobranchial filaments 0, precaudal vertebrae 13 (12), caudal vertebrae including urostyle 29 (32). Measurements in % SL: HL 21.4 (24.2), predorsal length 26.6 (29.3), preanal length 49.3 (46.2), body depth at dorsal fin origin 13.5 (15.9), body depth at vent 11.5 (13.7), head width 5.9 (8.6), pectoral fin length 8.7 (11.3), pelvic fin length 11.9 (13.7). Measurements in % HL: eye diameter 5.6 (5.6), snout length 22.2 (21.1), maxillary length 48.1 (48.9), fleshy interorbital width 18.5 (22.2).

Head and body compressed, tail not tapered posteriorly (Fig. 1). Head small, slightly less than 1/2 preanal length. Snout round from lateral view, slightly projecting beyond upper jaw (Fig. 2a). Eye small, about

1/4 snout length. Anterior nostril tubular, just above upper lip. Posterior nostril small, rounded, slightly before anterior margin of eye, at mid-eye level. Mouth large, nearly horizontal. Maxillary extending backward far behind posterior margin of eye, its posterior end rounded, not sheathed by dermal cheek fold, without ventrally-directed process near its postero-ventral corner. Lower jaw included in upper jaw. Opercular spine flat and weak, completely covered by skin. Posterior and lower margins of preopercle smooth, completely covered by skin. Gill opening wide; gill membranes united slightly behind posterior margin of eye, free from isthmus. Pore-bearing skin flap absent from just above upper angle of gill opening. A single pore with short tube in front of upper angle of gill opening. Infraorbital pores four; three large, slit-like pores between slightly behind anterior nostril and just below posterior nostril, a single, small pore above posterior end of maxillary. Supraorbital pore single, large, on underside of snout tip before anterior nostril (Fig. 2b). Two mandibular pores on each side; left and right anterior pores separated, left and right posterior pores united on ventral mid-line of head. A single, small pore near lower angle of preopercle.

All teeth sharp-pointed (Fig. 3). Upper jaw teeth uniserial, becoming longer anteriorly, needle-like. Lower jaw teeth biserial, inner teeth larger. About six teeth on vomer, uniserial, well separated, nearly equal to inner teeth on lower jaw. Palatine teeth about five, uniserial, slightly shorter than vomerine teeth. Tongue short, its tip bluntly pointed, free from mouth floor.

Developed rakers on anterior arch three, short, about equal in length to eye diameter. Pseudobranchial filaments absent.

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Fig. 3. Upper and lower dentition of NTM S.14665-026, holotype of *Acarobythites larsonae* sp. nov. Scale bar indicates 0.5 mm.

Dorsal fin originating above mid-length of pectoral fin. Origin of anal fin at about mid-body. Pectoral fin short, no separated or free rays. Pectoral peduncle normal, broader than long. No spine on posterior margin of cleithrum. Pelvic fins not reaching to below tip of pectoral fin, closely adjacent at their bases, inserted slightly behind posterior margin of preopercle.

Head and body covered with mucous coating, completely devoid of scales. Tiny papillae sparsely present on anterior half of head. Lateral line indistinct.

Tips of neural spines of precaudal vertebrae pointed; first neural spine short, 2nd spine longest, erect, 5th to 11th spines short, well depressed (Fig. 4).

In alcohol, head and body uniformly creamy-yellow, slightly darker on dorsum of head and body, paler on belly. All fins and buccal cavity pale.

Distribution. Known only from the type locality (Field Island) and Cobourg Peninsula, western Arnhem Land, Northern Territory, Australia.

Etymology. Named *larsonae* after Dr. Helen K. Larson (NTM), who kindly sent me valuable bythitid and ophidiid specimens for study.

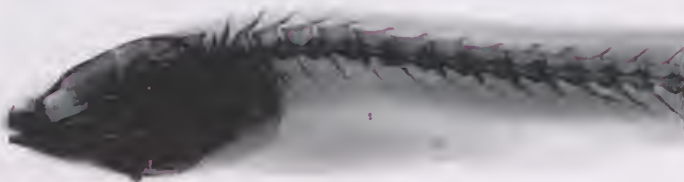


Fig. 4. Positive image of X-ray photograph of NTM S.14665-026, holotype of *Acarobythites larsonae* sp. nov.

Six new species of fork-tailed catfishes (Pisces, Teleostei, Ariidae) from Australia and New Guinea

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ABSTRACT

Six new species of *Arius* (Teleostei: Ariidae) are described from estuarine waters of southern New Guinea and northern Australia. *Arius dioctes* sp. nov. is present in both regions and is distinguished by its large maximum size, small eyes, fixed (non-depressible) jaw teeth, broad mouth, and yellow lower body. *Arius insidiator* sp. nov. has a much depressed body, long, angular ribs, small eyes covered by skin and fixed jaw teeth. It too has a yellow lower body. *Arius pectoralis* sp. nov. is a slender catfish with strong, numerous serrae along the hind margin of the pectoral spines and dark margins on the dorsal, pectoral and the caudal fins. *Arius hainesi* sp. nov. has fleshy lips, small mouth, partly restricted gill openings, short barbels, ridges in the skin on the back below the dorsal fin, and often a dark mouth and branchial chamber. The barbels of *Arius hardenbergi* sp. nov. are thick proximally. This species also has a fleshy snout, an extensive head shield with broad supraoccipital process and a long-based adipose fin. *Arius paucus* sp. nov. is a freshwater species very similar to *Arius midgleyi* Kailola and Pierce and inhabits the river systems draining into the Gulf of Carpentaria.

KEYWORDS: Ariidae; fork-tailed catfishes; new species; Australia; New Guinea; tropical marine; tropical freshwater.

INTRODUCTION

The isolation of the Sahul Shelf has enabled the evolution of many endemic species of fork-tailed catfishes (Ariidae). These fish inhabit the rivers, estuaries and coastal waters of tropical (northern) Australia and New Guinea. Earlier workers (e.g. Roberts 1978; Haines 1979; Coates 1983, 1988; Allen and Coates 1990) have remarked on the adaptive characteristics of these ariids.

The Ariidae occurs worldwide in tropical and warm-temperate regions. It comprises at least 80 valid species and numerous nominal genera and species, many confined to particular geographic regions (west Africa, east Africa to India, South-east Asia, Australia-New Guinea, eastern Pacific, western Atlantic). The phylogenetic relationships of the family are under study.

Thirty-five species of ariid catfishes inhabit Australian and New Guinea waters and only five of these, all marine catfishes (*Arius thalassinus* Rüppell, 1837; *A. bilineatus* Valenciennes, 1840a; *A. argyropleuron* Valenciennes, 1840b, *A. nella* (Valenciennes, 1840b) and *A. polystaphylodon* Bleeker, 1846), occur elsewhere; in South-east Asian, Indian and east African (*A. thalassinus*) seas (Kailola 1990b). Of the remaining 30 taxa, five species (*A. nox* Herre, 1935; *A. solidus* Herre, 1935; *A. coatesi* Kailola, 1990a; *A. utarus* Kailola, 1990a; and *A. velutinus* (Weber, 1908)) are endemic to

northern New Guinea fresh waters, and 12 species are endemic to southern New Guinea fresh and saline waters (Kailola 1990b). Eleven more species are common to both northern Australia and southern New Guinea. Only two species - *Arius midgleyi* Kailola and Pierce and a new species - are endemic to Australia.

The Ariidae are under-represented in collections. Most species attain moderately large size and it is sometimes not easy for field workers to keep intact material. Moreover, surveys have only been conducted since the mid-1970s in some of the areas which now reveal new species. The haphazard nature of ariid collecting in often difficult environments has created the paradox, however, that two of the endemic ariids from New Guinea described in 1913 by Weber (*Doiichthys novaeguineae* and *Tetranesodon conorhynchus*) are represented today by less than ten specimens. Yet the distribution of these taxa spans the most intensively collected aquatic habitats of southern New Guinea.

I recognised nine Australo-Papuan ariid catfish taxa as new several years ago and three of them were described subsequently (Kailola and Pierce 1988; Kailola 1990a). Although I acknowledge the need of a phylogenetic review and comprehensive key to the species of this region, my objective here is to describe six new species. The other information will be published elsewhere.

METHODS

Abbreviations (such as for head length, standard length, gill rakers) and definition of ariid features and relevant osteology have been described in Kailola (1983). Method of counting and measuring are defined in Kailola (1983) and Kailola and Pierce (1988). The term 'colour of fresh material' refers to freshly dead (just caught) or chilled specimens except for *A. insidiator*, where 'fresh colour' refers to frozen specimens. The term 'serrae' refers to large, regularly-spaced serrations.

Institutional abbreviations follow Leviton *et al.* (1985) and are: AMS (Australian Museum, Sydney); CSIRO (Ian S.R. Munro Ichthyological Collection, CSIRO, Hobart); KFRS (Kanudi Fisheries Research Station collection, Port Moresby, Papua New Guinea); NTM (Museum and Art Gallery of the Northern Territory, Darwin); QM (Queensland Museum and Art Gallery, Brisbane); USNM (United States National Museum, Smithsonian Institution, Washington); WAM (Western Australian Museum, Perth); ZMA (Zoölogische Museum, Universiteit van Amsterdam, Amsterdam).

KFRS material of these new species identified ten years ago generally is not included in the type series as the present whereabouts and condition of the material is unknown. However, an exception was made for two new species because of the paucity of material.

SYSTEMATICS

Arius dioctes sp. nov.

(Figs 1-2; Tables 1-2)

Hexanematichthys sp - Kailola 1975: 41 (in part).

Hexanematichthys sp 'Y' - Kailola and Wilson 1978: 42.

Arius cf. *stirlingi* - Roberts 1978: 37, fig.16a.

Arius sp. - Maunsell and Partners 1982: 181. - Allen 1991: 56, photo 14.

Arius (*Hemiaris*) species 1 - Kailola 1990b: 299.

Hemiaris sp.1 - Blaber, Brewer and Salini 1994: 163, fig 3a.

Type material. HOLOTYPE - CSIRO C.3798, 430 mm SL, Norman River at Karumba (17°29' S, 140°50' E), Queensland, D. J. Turner, 1969. PARATYPES - NTM S.11190-001, 2 (450-460 mm SL), Fog Bay (12°54' S, 130°14' E), Northern Territory, P. Mundy, June 1983; AMS I.15557-041, 2 (103-172 mm SL), Gulf of Carpentaria at 17°26' S, 140°40' E., I.S.R. Munro, 23 December 1963; AMS I.29292-001, 159 mm SL, Gulf of Papua (08°00' S, 145°00' E), S. Frusher, 11 July 1981; CSIRO H.5154-01, 1050 mm SL, Papua (Irian Jaya) at 04°49' S, 137°00' E, K. Hortle and A. Haris, 7 December 1996; NTM S.14828-005, 95.1 mm SL, Papua (Irian Jaya) at 04°55' S, 137°15' E, K. Hortle and A. Haris, 28 May 1998; KFRS F.04094, 200 mm SL, off Oreke River

mouth (08°42' S, 146°29' E), Papua New Guinea, J. Koaia, May 1973.

Additional material examined (non-type). KFRS F.5627-01, 350 mm SL, Tirere village, north side of Daru Island (09°05' S, 143°12' E), Papua New Guinea, April 1988; KFRS F.5626-03, 330 mm SL, Sagero, north side of Daru Island, Papua New Guinea, September 1988; KFRS F.5729-03, 166 mm SL, Daru Island, Papua New Guinea, 30 September 1983; KFRS FO3992, 10 (84-89 mm SL), Pic River at Baimuru (07°33' S, 144°51' E), Papua New Guinea, 28 September 1971 (juveniles from mouth of an adult male, 104 cm SL); KFRS F04099, 328 mm SL, old Kukipi village, Lakekamu River mouth (08°12' S, 146°10' E), Papua New Guinea, 18 October 1971; CSIRO H.4957-01, 4 (86-94 mm SL), Papua (Irian Jaya) at 04°55' S, 137°03' E, K. Hortle and A. Haris, 28 May 1998; CSIRO H.4976-04, 325 mm SL, Papua (Irian Jaya) at 04°53' S, 136°55' E, 6 September 1997.

Diagnosis. Teeth very strong, non-depressible; in narrow bands in jaws and in four patches arranged across front of palate. Snout prominent, jaw teeth exposed; mouth wide. Head somewhat venulose, head shield almost smooth. Eye small, free of head skin, 6-14 % HL; few (10-11) first arch gill rakers; no rakers on posterior face of first two arches; gill opening wide. Body orange-yellow; lips, inside mouth and body usually covered with orange or yellow mucus, and teeth frequently reddish.

Description. D 17. P I, 11-12. A 17-21. GR (first arch) 10-11 of which 3-4 on upper limb. GR (last arch) 9-11. Vertebrae 49-50 (42-43 free).

Body robust anteriorly, tapered, well compressed posteriorly. Predorsal profile straight becoming convex at nape. Snout prominent, well-rounded; inner lip margin scalloped. Jaws strong; mouth wide, curved, subterminal or inferior. When mouth closed, tooth band in upper jaw almost completely exposed, outer rows of lower jaw teeth also visible. Nostrils large, ovate, anterior one directly before posterior one. Eye ovate, moderately small, border completely free from head skin; eye dorsolateral, well before mid-head length. Gill opening wide, membranes broadly scalloped, meeting at sharp angle, leaving broad, free margin.

All teeth sharp, strong, conical, not depressible. Premaxillary tooth band with 4-6 irregular series of teeth; mandibular tooth band with 4-5 series of teeth, almost continuous across symphysis. Four patches of teeth in row across anterior of palate: two inner (vomerine) patches separated by narrow gap at midline, half as wide as outer, curved patches; 3-4 rows of teeth in each group. Palate smooth anteriorly, longitudinally creased posteriorly, with two long, low ridges of epithelial tissue before branchial chambers.

Head shield smooth anteriorly; several groups of sharp granules laterally, distinct parallel striae adjacent to distal third of dorsomedian head groove, striae

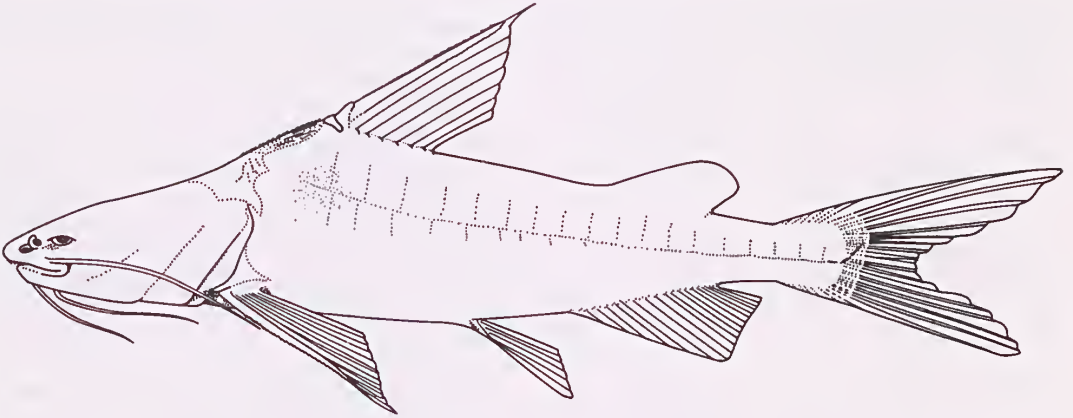


Fig. 1. *Arius dioctes* sp. nov. lateral view, 200 mm SL paratype.

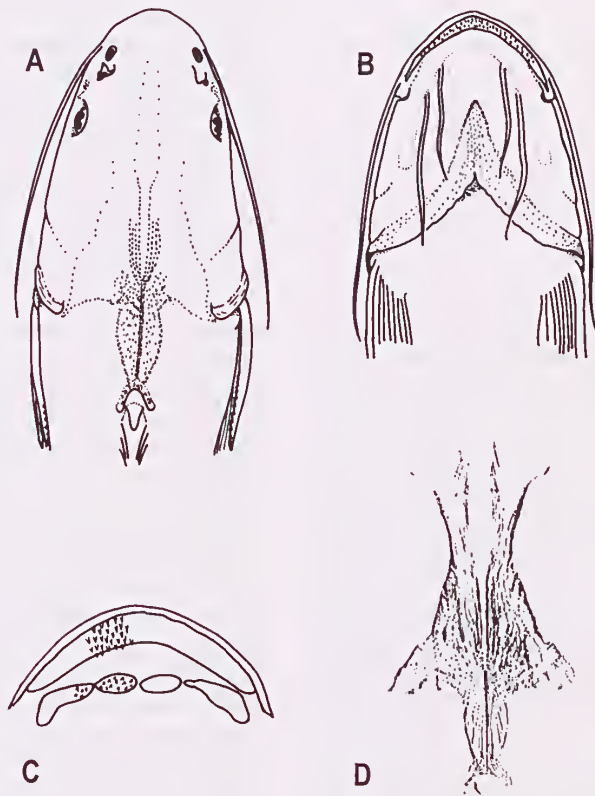


Fig. 2. *Arius dioctes* sp. nov. (all 200 mm SL paratype) A, dorsal head view; B, ventral head view; C, arrangement of upper tooth patches; D, rubbing of head shield.

Table 1. Principal meristics of six new species. n = number; \bar{x} = mean, SD = standard deviation; GR 1 = rakers on first gill arch; GR 4 = rakers on last gill arch.

Species	variable	Anal rays	Pectoral rays	Total GR 1	Total GR 4
<i>A. dioctes</i>	holotype	20	12	10	10
	range, n = 9	17-21	11-12	10-11	9-11
	\bar{x}	18.7	11.6	10.3	10.0
	SD	1.4	0.5	0.5	0.7
<i>A. insidiator</i>	holotype	20	10	12	12
	range, n = 4	19-23	10	11-12	11-13
	\bar{x}	20.5	10.0	11.5	11.5
	SD	1.7	0.0	0.6	0.8
<i>A. pectoralis</i>	holotype	18	8	15	15
	range, n = 16	18-22	8-11	15-22	14-17
	\bar{x}	19.3	10.0	18.8	15.3
	SD	1.2	0.9	1.8	1.1
<i>A. hardenbergi</i>	holotype	18	10	14	13
	range, n = 5	16-18	9-10	10-14	9-13
	\bar{x}	16.6	9.4	11.2	9.8
	SD	0.9	0.5	1.6	1.8
<i>A. hainesi</i>	holotype	20	10	32	36
	range, n = 14	20-23	8-11	32-37	31-37
	\bar{x}	21.7	9.6	34.3	33.5
	SD	0.7	0.8	1.4	1.7
<i>A. paucus</i>	holotype	17	10	11	13
	range, n = 16	16-18	9-10	10-11	11-14
	\bar{x}	17.3	9.9	10.7	12.8
	SD	0.8	0.3	0.5	0.8

extending over supraoccipital process. Dorsomedian groove narrow, lanceolate, flat, extending from between nostrils to supraoccipital process base. Supraoccipital process with sharp, distinct keel, straight to slightly convex sides. Predorsal plate angular, striate. Numerous, anastomosing venules over anterior two-thirds and sides of head, continuing onto shoulder. Rugose humeral process anteroventrally well ossified, forming narrow flange; acute, triangular shaft of process reaching one-quarter to one-third along pectoral fin spine. Axillary pore small and slit-like.

Barbels thin distally. Maxillary barbel attains end of humeral process in juveniles, to well before opercular margin in adults. Mandibular barbel reaches opercular margin in young, preopercular margin in adults. Mental barbel extends short distance behind eye. Chin barbel bases staggered.

Gill rakers rigid, pungent, half to two-thirds length of opposing filaments. No rakers along posterior face of first two gill arches, 9-11 along posterior face of third arch. Low, muscular thickening posterodorsally on smooth arches.

Fin spines thick, slightly curved, rounded, patterned with fine rugae and granules. Anterior margin of spines with distinct granules proximally, 6-10 antrorse, low

serrae distally; posterior margin with 8-30 serrae or denticles. Short filament on spine tips. Longest dorsal ray 1.9-3.2 times longer than last ray. Pectoral fin low, extending to below dorsal fin. Ventral fin narrow in males, ending well before anal fin origin. Fin in females broad, attains anal origin or beyond (inner rays thicken and form pad of tissue in sexually mature individuals). Adipose fin moderately high, oblong, originating approximately opposite anal fin origin. Anal fin margin almost truncate, longest ray 2.1-3.6 times last ray. Caudal fin lobes broad-based, strongly tapered, upper lobe slightly longer than lower.

Caudal peduncle shallow. Lateral line straight, oblique below dorsal fin, strongly upturned at tail base. Short lines and ascending rows of pores branch off from lateral line, numerous and extensive anteriorly.

Colour of fresh material. Greenish or pale bluish grey above; pale orange or yellow on sides and below, less often cream or white. Bright yellowish orange mucus over all of body; lips and inside of mouth also yellow. Barbels and teeth reddish or yellow. Fins bluish grey, green or yellowish, dusky towards margins. Snout and head of some individuals blotched black.

Colour of preserved material. Pinkish brown or tan above, cream or pale fawn below, top of head darker brown. Fins brown or light tan, margin of dorsal fin and caudal fin dark brown; upper aspect of pectoral fin, ventral fin and mid-anal fin rays darker brown. Maxillary barbel dark brown, others pale. Peritoneum grey.

Comparisons. *Arius dioctes* is similar to *A. stormii* (Bleeker, 1858), a South-east Asian species growing to over 50 cm long (Weber and de Beaufort 1913). However, *A. stormii* possesses the following unique features: dorsal spine subequal to head length (versus equal to head length without snout in *Arius dioctes*); caudal peduncle depth 2.6-2.8 in its length (versus 1.9-2.3 in *Arius dioctes*); anterior nostrils lateral to posterior ones (versus anterior to posterior nostrils in *Arius dioctes*); total gill rakers on the first arch 17-18 (versus 10-11 in *Arius dioctes*); serrae on front margin of dorsal spine directed upwards (versus directed downwards in *Arius dioctes*); fin spines very broad (versus moderately broad in *Arius dioctes*); adipose fin beginning before anal origin (versus opposite or behind in *Arius dioctes*).

The most phenotypically similar species to *Arius dioctes* in Australia and New Guinea is *A. armiger* De Vis, 1884 (distinguished by its venulose head, small eye and strong teeth). The taxa can easily be distinguished however, on gill raker and anal fin meristics (*A. armiger* has GR16-22, first arch; A 22-25) and maxillary barbel length (long maxillary barbel reaches at least to below dorsal fin). *Arius dioctes* has similar colouration and dentition to *Arius insidiator* sp. nov. However, the form of the body easily distinguishes these two taxa.

Distribution. *New Guinea:* southern coast and rivers from Kamora River to the Otokwa River, possibly also

Table 2. Percent of head length (HL) and standard length (SL) for *Arius dioctes* sp. nov. and *Arius insidiator* sp. nov. n = sample size; \bar{x} = mean; SD = standard deviation.

Character	<i>Arius dioctes</i>					<i>Arius insidiator</i>				
	holotype	n	range	\bar{x}	SD	holotype	n	range	\bar{x}	SD
Percent of HL										
head height	38.1	9	38.1 - 50.0	42.9	4.0	39.8	4	35.0 - 39.8	37.7	2.3
head width	66.3	9	61.3 - 71.3	66.3	2.9	64.1	4	61.9 - 64.9	64.4	2.0
eye diameter	6.8	9	5.7 - 13.2	8.8	2.5	6.0	4	5.6 - 6.8	6.0	0.5
mouth gape	47.3	9	44.7 - 52.3	47.4	2.5	44.3	4	42.8 - 45.8	44.0	1.2
internostil distance	35.7	9	33.1 - 35.9	34.8	1.1	31.4	4	31.4 - 34.7	32.4	1.5
snout length	34.7	9	32.2 - 37.2	34.4	1.5	27.8	4	27.8 - 31.6	29.0	1.8
longest barbel length	54.4	9	40.7 - 77.4	61.3	13.2	32.4	4	32.4 - 52.0	40.1	8.5
bony interorbital width	33.1	8	26.6 - 35.4	31.7	3.2	25.8	4	25.8 - 27.8	26.5	0.9
occipital proc. length	28.1	9	25.5 - 34.4	29.6	2.6	28.8	4	28.8 - 36.9	33.0	3.5
occipital proc. width	18.4	9	13.7 - 21.8	16.9	3.2	10.1	4	8.3 - 15.1	10.8	3.0
Percent of SL										
HL	31.4	9	31.4 - 34.7	32.5	1.1	32.6	4	29.8 - 32.6	31.1	1.2
head height	12.0	8	12.0 - 16.3	14.0	1.4	13.0	4	10.6 - 13.0	11.7	1.0
head width	20.9	9	19.5 - 22.9	21.5	1.0	20.9	4	18.8 - 21.1	20.0	1.1
eye diameter	2.1	9	2.0 - 4.0	2.8	0.7	1.9	4	1.8 - 2.1	1.9	0.2
mouth gape	14.9	9	14.2 - 16.5	15.4	0.7	14.4	4	13.0 - 14.4	14.0	0.6
internostil distance	11.2	9	10.7 - 12.3	11.3	0.5	10.2	4	9.4 - 11.0	10.1	0.7
snout length	10.9	9	10.5 - 12.3	11.2	0.6	9.1	4	8.5 - 10.0	9.0	0.7
longest barbel length	17.1	9	14.1 - 24.7	19.9	4.2	10.5	4	10.5 - 16.4	12.5	2.7
bony interorbital width	10.4	8	8.5 - 11.4	10.3	1.1	8.4	4	7.9 - 8.4	8.2	0.3
occipital proc. length	8.8	9	8.7 - 10.9	9.6	0.8	9.4	4	9.4 - 11.2	10.2	0.8
predorsal length	39.4	9	39.4 - 42.8	41.1	1.1	37.3	4	35.4 - 37.3	36.3	0.9
length dorsal f. base	10.8	9	10.0 - 13.2	11.6	0.9	10.3	4	10.3 - 12.2	10.3	0.9
interdorsal length	22.8	9	21.6 - 25.7	23.6	1.3	28.8	4	25.1 - 28.8	6.0	0.4
length adipose f. base	10.4	9	8.0 - 12.3	10.4	1.4	9.0	4	9.0 - 11.1	10.0	0.9
length anal f. base	16.9	9	13.3 - 16.9	15.3	1.3	15.1	4	15.1 - 17.0	16.0	0.9
caudal ped. depth	6.5	9	6.5 - 7.3	6.9	0.3	6.3	4	6.2 - 7.1	6.5	0.4
caudal ped. length	13.8	9	11.2 - 17.7	14.4	2.0	14.5	4	13.3 - 15.0	14.3	0.7
pectoral spine length	19.5	8	17.3 - 21.3	19.6	1.6	15.0	4	15.0 - 16.4	16.0	0.6
dorsal spine length	21.8	8	17.1 - 23.2	21.1	2.4	16.8	4	15.6 - 18.3	16.9	1.3

further westward and in intermediate rivers; from there eastwards to the middle and lower river and delta of the Fly, throughout the Gulf of Papua rivers including the Kikori, Era, Pie and Purari systems and deltas, Vailala River mouth, Murua River, Lakekamu and Oreke Rivers. *Australia*: northern coast and rivers from the Adelaide and Alligator Rivers to the Gulf of Carpentaria and the Norman River.

Ecology. Coastal and lower mangrove areas, estuaries into main rivers and lagoons; also freshwater.

Remarks. In late 1976, this species was the second most important commercial species at Kikori (Papua New Guinea) after barramundi (*Lates calcarifer* (Bloch) (Haines 1979). *Arius dioctes* has been recorded to attain 1.2 m SL (Roberts 1978) and 19 kg whole weight (T. Coleman pers. comm.). Papuan villagers report that this species can attain 2 m in length. N. Haysom and T. Davis (pers. comm.) have collected 1-2 m, 'up to 40 kg' fish from the Alligator and Norman rivers. The 1050 mm SL paratype from Papua (Irian Jaya) weighed c. 15 kg when fresh.

Etymology. *dioctes*, masculine. From the Greek, *dioktes*, meaning hunter or pursuer - in reference to the species' apparent hunting ability, diet and dentition.

Arius insidiator sp. nov.

(Figs 3-4; Tables 1-2)

Hexanematichthys sp - (in part) Kailola 1975: 41.

Hexanematichthys sp 'D' - Kailola and Wilson 1978: 40, 42.

Arius (*Hemiaris*) species 5 - Kailola 1990b: 306.

Type material. HOLOTYPE - NTM S.11189-001, 350 mm SL, mouth of Wildman River (12°26' S, 132°09' E), Northern Territory, P. Mundy, 28 February 1984. PARATYPES - AMS I.28960-001, 282 mm SL, Gulf of Papua (08°00' S, 145°00' E), S. Frusher, 1978; KFRS F.03302, 188 mm SL, half mile inside Pai'a Inlet (07°39' S, 144°33' E), Papua New Guinea, F.R.V. *Tagula*, 6 May 1967; KFRS F.5526-01, 270 mm SL, off Kerema (07°58' S, 145°43' E), D. Whitten, D. Coates and R. Watson, 11 October 1983.

Diagnosis. Head and anterior of body depressed; ribs long, angular, impressed in abdominal body wall. Eye covered with head skin; head smooth. Mouth wide, terminal, jaws upturned at symphysis; teeth fixed, cardiform, in 1-2 series on jaws and palate; four elongate patches of palatal teeth. No rakers on posterior of first two arches; mandibular barbel longest, reaching dorsal fin. A 19-23; total gill rakers (first arch) 11-12; total vertebrae 24+3+33. Fin spines slender, weak. Fresh

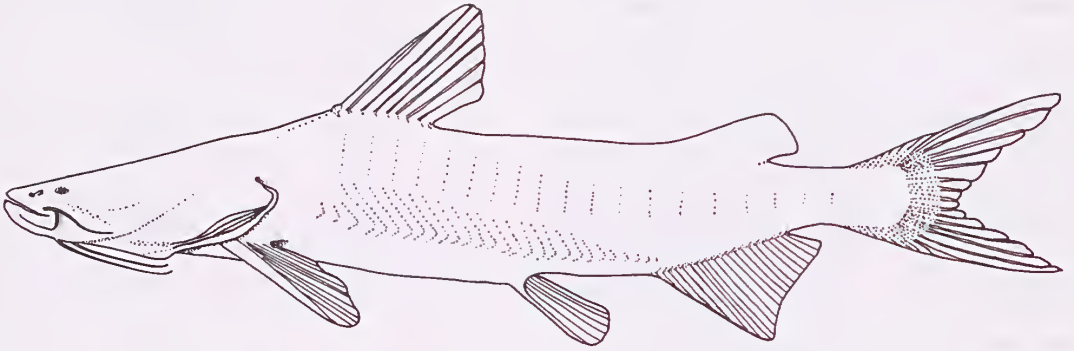


Fig. 3. *Arius insidiator* sp. nov. lateral view, holotype

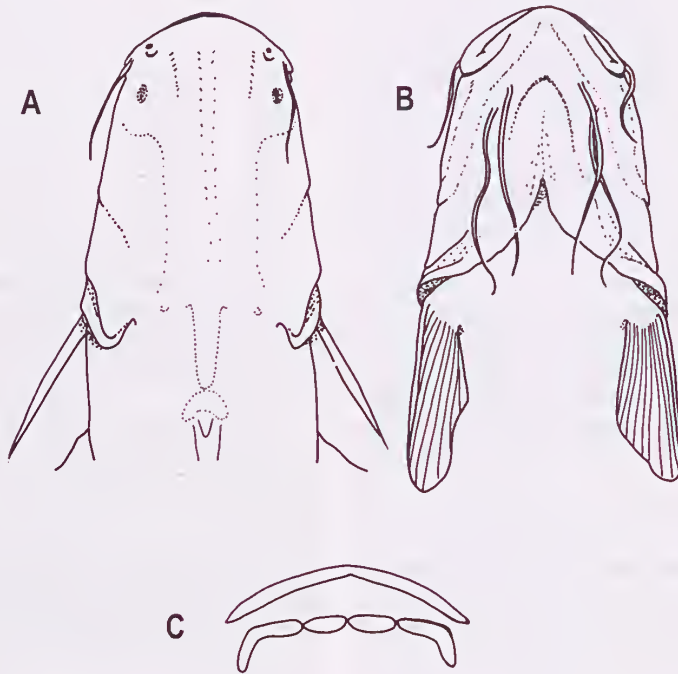


Fig. 4. *Arius insidiator* sp. nov. A dorsal head view; B, ventral head view (both of holotype); C, arrangement of upper tooth patches (188 mm SL paratype).

colouration grey or yellowish, fins and mouth (bright) yellow or orange.

Description. D 1,7. P 1,10. A 19-23. GR (first arch) 11-12, of which 5 on upper limb. GR (last arch) 11-13. Vertebrae 58-60 (51-54 free).

Body moderately stout, anterior two-thirds depressed; angular pleural ribs of trunk and anterior caudal vertebrae apparent through body wall, forming a 'shelf' along lower sides. Predorsal profile almost straight. Snout evenly rounded; lips narrow, much thickened at corners, scalloped along inner margin. Jaws strong, lower jaw elevated at symphysis, slightly longer than upper; mouth terminal to superior, broad, curved; teeth not visible when mouth closed. Nostrils small, rounded, placed well forward on snout; anterior one directly in front of posterior one. Eye ovate, small, covered with head skin, almost dorsally situated and about four eye diameters before mid-head length. Gill opening wide, membranes meeting well forward; distal margin broad.

Teeth fixed, strong, slightly curved, cardiform. Teeth on both palate and upper jaw arranged in two (rarely one) row(s) with distinct naked space between rows, teeth in inner row longer. One row of teeth on lower jaw; naked space at symphysis. Four elongate patches of teeth across palate: inner pair adjoining and half as wide as curved outer patches. Palate smooth; two long, low ridges of epithelial tissue before branchial chamber.

Head shield completely smooth except for slightly roughened lateral margins. Dorsomedian head groove lanceolate, flat, beginning well forward on snout and almost reaching base of supraoccipital process. Process narrow, with straight sides, rounded from side to side. Sides of head smooth. Broad-based, triangular humeral process smooth, weakly ossified anteroventrally, its shaft short, oblique, extending one quarter distance along pectoral spine. Axillary pore small.

Barbels thin, flattened. Maxillary barbel short, reaching only to preopercular margin. Mandibular barbel long, extending past head or as far as anterior dorsal rays. Mental barbel reaches ventral head margin or beyond pectoral base. Chin barbel bases clearly staggered.

Gill rakers stiff, moderately pungent, half as long as opposing gill filaments. Gill arches smooth; no rakers on posterior face of first two; 10-12 rakers along back of third arch. No thickened tissue posterodorsally on arches.

Fin spines feeble, rounded, pungent in smallest specimen; smooth or roughened along anterior margin, weakly serrated or roughened along posterior margin (smallest specimen with 8-9 serrae along posterior margin of pectoral spine). Dorsal fin truncate in outline, longest ray 2.3-2.8 times longer than last ray. Pectoral fin low on sides, its base in a horizontal plane; fin hind margin truncate above, concave below. Pectoral fin reaching to below dorsal. Ventral fin of both sexes broad,

terminating well short of anal fin origin. Adipose fin above anterior two-thirds of anal. Anal fin margin almost straight, longest ray 2.6-3.1 times last ray in length. Caudal fin lobes broad and short.

Caudal peduncle stout. Lateral line straight, curved dorsad at tail base. Numerous fine short lines emanate from lateral line, forming dense, branching network anteriorly. Indistinct vertical series of pores ascend from lateral line over upper sides.

Colour of fresh material. Pale grey to yellowish above, white below; colours well-separated. Barbels grey or cream; mouth 'honey'-coloured. Dorsal, ventral, anal and pectoral fins bright yellow-orange; caudal fin dull yellow-orange.

Colour of preserved material. Charcoal or dark lilac-brown above, upper jaw and undersides pale. Lower sides and underside of head cream or pinkish, colour extending dorsally along gill membranes; nostrils and eyes also in pale streaks. Dorsal, pectoral and ventral fins dusky yellow basally, charcoal distally or over dorsal aspect; anal and caudal fins dull yellow or pale orange. Peritoneum pale.

Comparisons. This species is distinct in dentition, body form and colouration. Its colouration is similar to that of *Arius dioces* and its strong teeth and small eyes link it to that species and to *A. armiger* De Vis, 1884. The only other species with a skin-covered eye is *Doiichthys novaeguineae* Weber, 1913 which also has an upturned mouth. Nevertheless, none of them have *A. insidiator*'s flattened body, peculiar swimbladder form (flattened and elongate versus cardiform and inflated) and angular pleural ribs.

Distribution. *New Guinea*: southern coast along the Gulf of Papua. *Australia*: northern coast east of Darwin. Probably more widespread (for example, individuals have been seined in the Fly River delta (C. Tenakanai, pers. comm.).

Ecology. Shallow mudflats and river mouths; muddy coastal waters.

Remarks. The holotype is the largest specimen known.

Etymology. Noun in apposition; from the Latin, *insidiator*, meaning ambusher or lurker. The dorsally placed eyes and depressed body form suggest that this species' habit is to lie half-hidden in sediment. Its strong teeth and jaws indicate it is a predator. Although large fish scales and detritus were adhering to the gills of the largest specimen, the stomachs of all were empty.

Arius pectoralis sp. nov.

(Figs 5-6; Tables 1, 3)

Arius species 3 - Kailola 1990b: 397.

Arius sp. 3 - Blaber, Brewer and Salini 1994: 168, fig. 3m.

Type material. HOLOTYPE - AMS I.27415-001, 226 mm SL, Chapman River, Queensland (14°56' S,

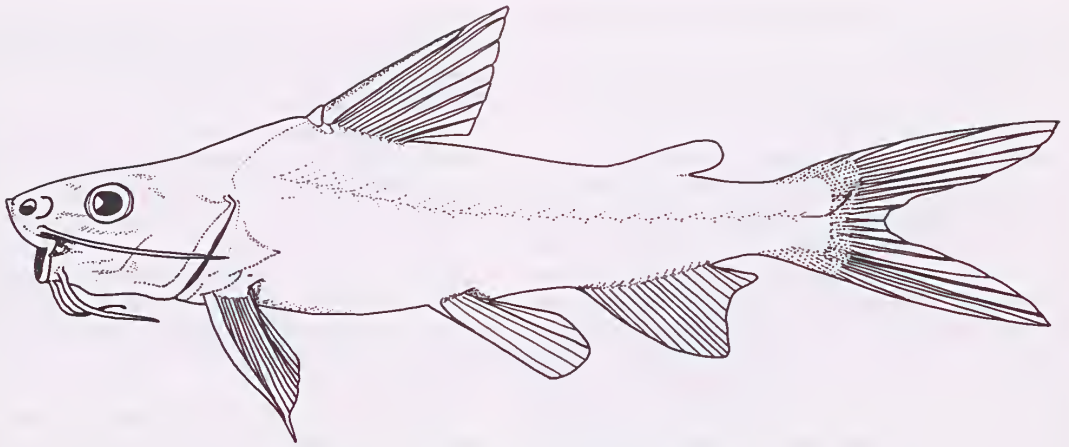


Fig. 5. *Arius pectoralis* sp. nov. lateral view, holotype.

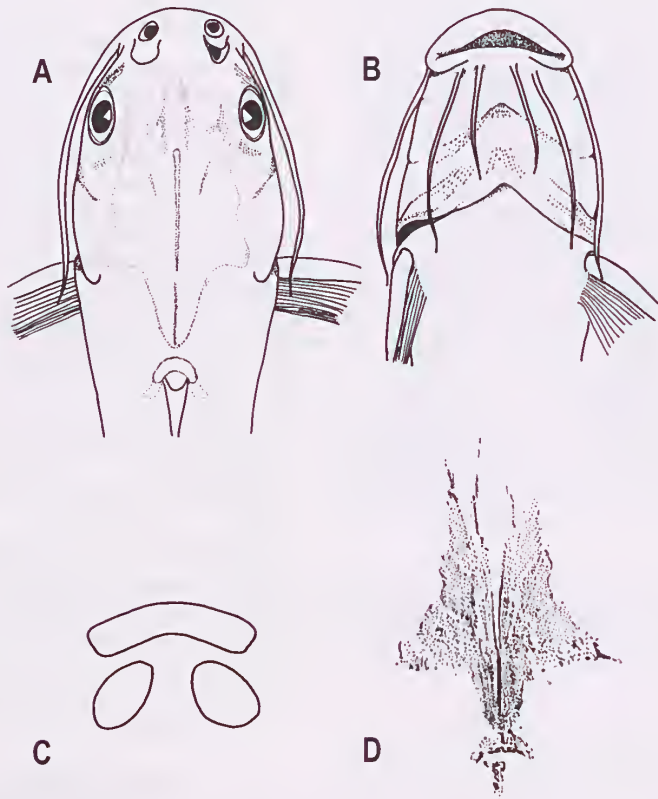


Fig. 6. *Arius pectoralis* sp. nov. (all of holotype) A, dorsal head view; B, ventral head view; C, arrangement of upper tooth patches, D, rubbing of head shield.

141°38' E), D.B. Carter, 21 December 1980. PARATYPES - NTM S.13004-001, 127 mm SL, Chapman River, Queensland, D.B. Carter, 5 March 1981; CSIRO A.3608, 112 mm SL, Norman River above Karumba, Queensland (17°29' S, 140°50' E), I.S.R. Munro, 22 October 1972; CSIRO A.3609, 117 mm SL, same data as A.3608; CSIRO A.3610, 116 mm SL, same data as A.3608; QM I.14917, 105 mm SL, Darwin Harbour (12°27' S, 130°46' E), November 1972; NTM S.10254-001, 2 (94.5-101 mm SL), Mickett Creek, Shoal Bay, Melville Island, Northern Territory (12°21' S, 131°00' E), D. Grey, 16 December 1976; NTM S.10319-003, 56 mm SL, Shoal Bay, Melville Island (11°48' S, 130°39' E), D. Grey, 19 October 1972; NTM S.10235-001, 90 mm SL, Shoal Bay, Melville Island, D. Grey, 1 August 1973; NTM S.11507-004, 145 mm SL, Ludmilla Creek, Darwin (12°27' S, 130°46' E), G. Cole and A. Howard, 19 December 1984; CSIRO H.5174-07, 4 (165-180 mm SL), Papua (Irian Jaya) at 04°52' S, 136°57' E, K. Hortle and A. Haris, 6 September 1997; CSIRO H.4937-02, 220 mm SL, Papua (Irian Jaya) at 04°52' S, 136°57' E, K. Hortle and A. Haris, 6 September 1997.

Additional material examined (non-type). CSIRO H.4220-03, 230 mm SL, Papua (Irian Jaya) at 04°52' S, 136°55' E, K. Hortle and A. Haris, 8 February 1996; NTM S.14852-001, 11 (46-64 mm SL), Papua (Irian Jaya) at 04°52' S, 136°57' E, K. Hortle and A. Haris, 1 June 1998.

Diagnosis. Palatal teeth conical, in two oblique, oval patches; one on each side of palate, well-separated. Snout acute; lips fleshy, crenulate; lower jaw truncate. Head shield finely granular; dorsomedian head groove lanceolate, narrow distally. Eye large, 17-28 % HL. Large, flattened serrae along inner margin of pectoral spine; caudal fin lobes slender, acute. A 18-22; total first arch GR 15-22; rakers present along posterior face of all gill arches; vertebrae 18+6+27. Distinct, blackish margin on dorsal, pectoral and inner caudal fins.

Description. D 1, 7. P 1, 8-11. A 18-22. GR (first arch) 15-22, of which 5-7 on upper limb. GR (last arch) 14-17. Vertebrae 51 (44 free).

Body moderately slender; predorsal profile straight. Snout moderately to slightly acute; lips fleshy, crenulate; short, transverse crescent often present on dorsum of snout between nostrils. Mouth subinferior, gape moderately large; upper jaw somewhat acute medially, lower jaw almost truncate. Anterior nostril slightly medial to posterior one. Eye large, border free from head skin, dorsolateral and slightly before mid-head length. Gill opening moderately wide, concave at isthmus, margin moderately broad.

Teeth in jaws fine, sharp, depressible, forming 7-8 irregular series in upper jaw and 4-6 series in lower jaw, bands either meeting or slightly separated at jaw midlines. Single large, oval patch of conical, blunt teeth

on each side of palate anteriorly, obliquely situated, well-separated. Palate smooth or slightly papillose; two oblique, low to moderately developed epithelial ridges posteriorly on palate.

Head shield finely granular. Dorsomedian head groove originates between nostrils and reaches supraoccipital process base. Groove flat, lanceolate anteriorly, narrow and straight posteriorly. Supraoccipital process triangular, straight-sided, with median keel. Triangular humeral process rugose, well-ossified anteroventrally, its shaft oblique, extending one-third along pectoral spine. Axillary pore small.

Barbels flattened, moderately thick, fleshy. Maxillary barbel extends slightly beyond dorsal fin in juveniles, to humeral process in adults. Mandibular barbel usually reaches pectoral fin spine base. Mental barbel reaches ventral head margin. Chin barbel bases slightly staggered.

Gill rakers short, one-third to half length of opposing filaments. Rakers present along posterior aspect of all arches: 6-7 (upper limb only) to 11-14 (total) on first arch; 13-18 along second; 11-16 along third. Often some papillae on first two arches. Fleshy, scalloped epithelial folds moderately developed posterodorsally on first two arches.

Fin spines strong, moderately long; sides with fine, longitudinal striae. Short filament on tip of spines. Anterior spine margin finely rugose with several sharp, antrorse serrae near tip; posterior (trailing) margin with low (dorsal spine) or large and flattened (pectoral spine) serrae: 8-11 along dorsal, 12-13 along pectoral. Last dorsal fin ray 2.9-3.4 times shorter than longest ray. Pectoral fin extends to below posterior dorsal fin rays. Ventral fin in males narrow, failing to reach anal origin by distance of half eye diameter; in females, broad-based, reaching to fourth anal ray (inner ventral fin rays thickened to form a pad in sexually mature female fish). Adipose fin rectangular, situated above middle of anal fin. Anal fin margin slightly concave, last ray 2.5-3 times shorter than longest ray. Caudal fin lobes slender, tapered, acute, upper lobe slightly longer.

Caudal peduncle moderately stout. Lateral line straight along sides, oblique below dorsal fin, turned dorsad at tail base. Fine, short lines of pores diverge off length of lateral line.

Colour of fresh material. Dark bluish brown or black above, white to cream below. Charcoal or black margin to fins (particularly caudal fin) and anterior two-thirds of anal fin also charcoal.

Colour of preserved material. Dusky fawn to charcoal above, creamy below; colours well-separated. Maxillary barbel usually dark. Unpaired fins and dorsal aspect of pectoral and ventral fins dusky or charcoal; distinct charcoal or black margin to inner caudal, dorsal and pectoral fins, and charcoal anal fin. Peritoneum pale, occasionally with scattered, dark stipples.

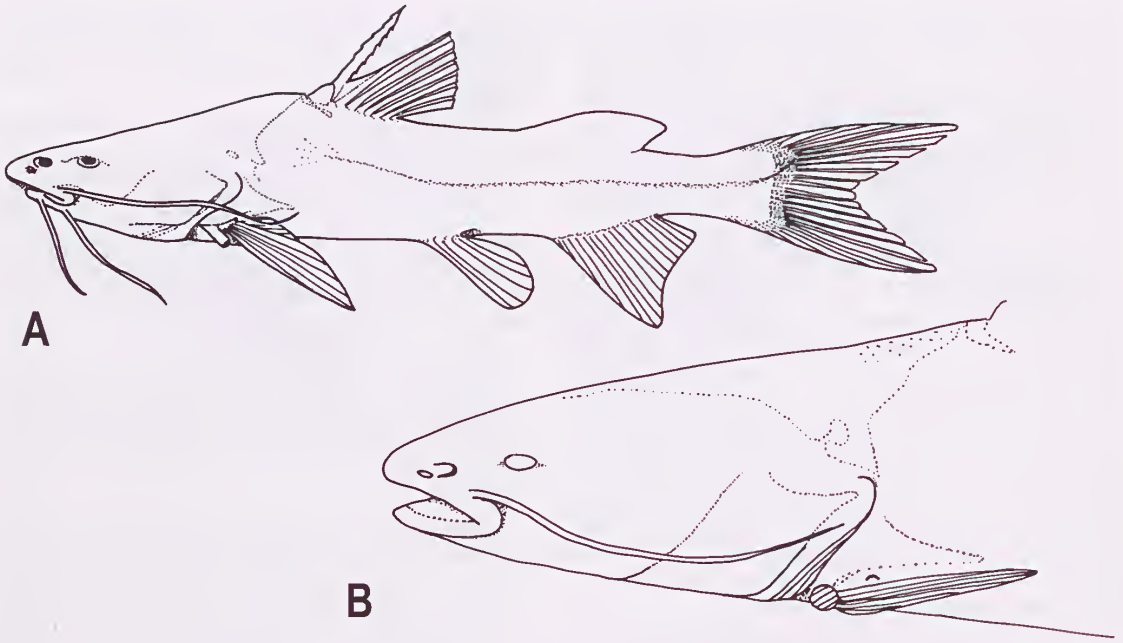


Fig. 7. *Arius hardenbergi* sp. nov. A, lateral view of 74.3 mm SL paratype; B, lateral head view of 253.8 mm SL paratype.

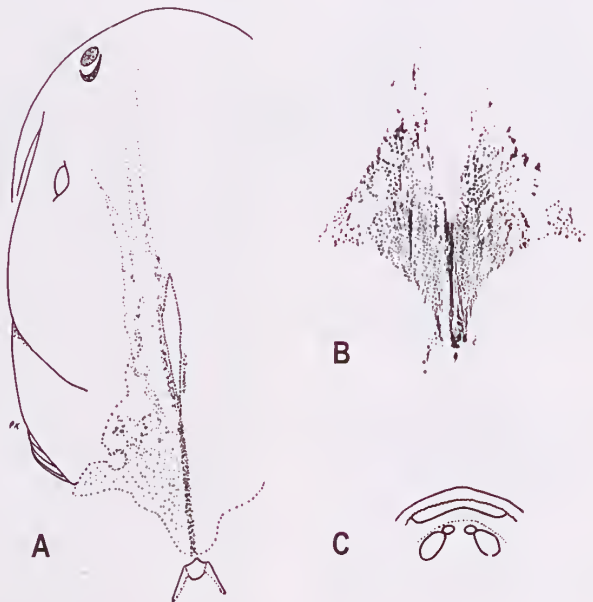


Fig. 8. *Arius hardenbergi* sp. nov. A, dorsal head view sketch of 253.8 mm SL paratype; B, rubbing of head shield, same paratype; C, arrangement of upper tooth patches, 74.3 mm SL paratype.

Table 3. Percent of head length (HL) and standard length (SL) for *Arius pectoralis* sp. nov. and *Arius hardenbergi* sp. nov. n = sample size; \bar{x} = mean; SD = standard deviation.

Character	<i>Arius pectoralis</i>					<i>Arius hardenbergi</i>				
	holotype	n	range	\bar{x}	SD	holotype	n	range	\bar{x}	SD
Percent of SL										
head height	60.9	16	51.0 - 64.4	58.9	4.8	47.0	5	47.0 - 55.6	51.0	3.1
head width	68.9	16	63.5 - 73.5	69.6	3.0	73.0	5	71.9 - 76.2	71.8	5.4
eye diameter	19.4	16	17.1 - 28.0	23.2	3.5	10.1	5	8.4 - 11.3	9.6	1.2
mouth gape	40.2	15	29.5 - 43.6	38.8	4.8	40.9	5	40.9 - 54.1	50.8	5.6
internostril distance	25.0	15	20.6 - 28.4	25.0	2.2	25.9	5	25.9 - 35.5	30.4	3.4
snout length	38.5	16	33.5 - 41.2	37.5	2.2	35.6	5	34.5 - 39.3	37.1	2.0
longest barbel length	79.9	15	78.0 - 121.7	101.0	13.1	76.7	5	76.7 - 110.5	86.6	23.2
bony interorbital width	29.4	15	26.3 - 33.0	29.8	2.0	31.7	5	29.9 - 34.3	32.1	1.9
occipital proc. length	28.2	15	28.2 - 38.2	33.9	2.5	-	4	26.9 - 41.6	31.5	7.3
occipital proc. width	19.4	15	18.7 - 26.0	21.8	2.8	-	4	5.4 - 34.1	18.2	12.0
Percent of SL										
HL	29.2	16	25.5 - 29.8	27.3	1.3	32.1	5	31.9 - 32.9	31.5	1.7
head height	17.8	16	14.4 - 17.8	16.1	1.0	15.1	5	15.1 - 17.9	16.5	1.1
head width	20.1	16	17.3 - 21.0	19.0	1.1	23.5	5	23.4 - 24.5	23.9	0.5
eye diameter	5.7	16	2.1 - 7.3	6.0	1.3	3.2	5	2.7 - 3.6	3.1	0.4
mouth gape	11.7	15	8.5 - 13.8	10.6	1.3	13.1	5	13.1 - 17.8	16.4	1.9
internostril distance	7.3	15	5.7 - 8.0	6.8	0.6	8.3	5	8.3 - 11.3	9.8	1.1
snout length	11.2	16	9.1 - 11.7	10.2	0.8	11.4	5	11.3 - 12.7	12.0	0.7
longest barbel length	23.3	15	22.4 - 32.8	27.5	3.1	24.6	5	24.6 - 36.1	30.4	5.5
bony interorbital width	8.6	15	7.1 - 9.8	8.2	0.8	10.2	5	9.8 - 11.0	10.4	0.5
occipital proc. length	8.2	15	8.2 - 10.6	9.3	0.8	-	4	3.0 - 14.1	8.5	4.5
predorsal length	37.9	16	35.2 - 40.0	36.9	1.5	42.0	5	39.2 - 42.0	40.5	1.3
length dorsal f. base	11.9	16	10.0 - 12.5	11.3	0.7	12.5	5	10.6 - 13.9	12.3	1.2
interdorsal length	27.7	16	16.5 - 33.7	28.2	3.7	26.2	5	14.3 - 26.2	18.5	5.1
length adipose f. base	8.5	16	6.7 - 11.5	8.5	1.3	12.1	5	11.7 - 18.9	16.0	3.7
length anal f. base	17.6	15	15.3 - 19.3	17.1	1.2	14.5	5	12.5 - 16.9	15.0	1.7
caudal ped. depth	8.0	16	7.1 - 8.7	7.9	0.5	7.6	5	6.9 - 7.8	7.4	0.4
caudal ped. length	15.9	16	15.2 - 20.2	17.0	1.2	14.8	5	14.6 - 17.8	15.9	1.3
pectoral spine length	19.8	15	19.5 - 26.0	21.4	1.7	21.8	3	17.3 - 21.8	19.9	2.3
dorsal spine length	21.7	14	19.0 - 27.3	21.9	2.0	15.3	4	15.3 - 18.8	16.9	1.5

Comparisons. *Arius pectoralis* is most similar to *Arius berneyi* (Whitley, 1941) and *A. graeffei* Kner and Steindachner, 1866, from which it can be distinguished by its more acute snout, palatal dentition (almost always a single patch on each side, compared with almost always two patches each side in *A. graeffei* and *A. berneyi*); also, palatal teeth finely conical instead of villiform in *A. graeffei* and *A. berneyi*), its strong pectoral spine serrae, very dark fin margins and slender caudal fin. *Arius pectoralis* differs from the only other taxon in the area with similar palatal dentition (*Cinetodus froggatti* (Ramsay and Ogilby, 1886)) by its wide gill opening and head shield form (restricted gill opening and very broad and high head shield in *C. froggatti*).

Distribution. *New Guinea*: south coast and estuaries of Papua (Irian Jaya) from the Kamora to Otokwa rivers. Probably occurs more extensively, in pockets, including the Port Moresby to the Kempwelch River area in central southern Papua New Guinea. *Australia*: Darwin (harbour and Ludmilla Creek) to Karumba and the Chapman River in Queensland.

Ecology. Coastal waters, estuaries and rivers within tidal influence; among mangroves.

Remarks. There are no literature records of this species, which has probably been confused in the field and earlier reports for *Arius berneyi* or *A. graeffei*. The maximum recorded size for *A. pectoralis* is 393 mm FL (Papua (Irian Jaya) specimen).

Etymology. From the Latin, *pectoralis*, meaning shoulder: refers to the strong serrae along the inner pectoral fin spine.

***Arius hardenbergi* sp. nov.**
(Figs 7-8; Tables 1, 3)

Arius species 6 - Kailola 1990b: 455.

Type material. HOLOTYPE - WAM P.29966-001, 260 mm SL, Manimcri River (02°06' S, 133°45' E), Bintuni Bay, Papua (Irian Jaya), G.R. Allen, 28 March 1989. PARATYPES - NCIP 436, 254 mm SL, Merauke (08°28' S, 140°20' E), Papua (Irian Jaya), J.D.F. Hardenberg, 4 August 1931; AMS I.29291-001, 2 (59.5-74.5 mm SL), delta of Fly River (08°22' S, 142°40' E), Papua New Guinea, J. Watson, 16-22 July 1981; QM I.26088, 56 mm SL, same data.

Additional material examined (non-type). NTM S.14873-001, 52 mm SL, Bamu River estuary, Papua New Guinea, at c. 08°08' S, 143°35' E, 21 June 1993.

Diagnosis. Four patches of conical teeth across front of palate; rounded vomerine patches well-separated; outer patches oval or crescentic, 2-3 times larger than inner patches. Snout fleshy, overhanging mouth. Low papillae on palate and posterior face of gill arches; rakers rarely on posterior face of first two gill arches. Barbels thick proximally, thin distally. Head shield very granular, extensive posteriorly; triangular supraoccipital process short, broad. Eye small, dorsolateral, 8-12 % HL. A 16-18; total gill rakers (first arch) 10-14; vertebrae 19+5+26. Adipose fin large, base longer than anal fin base. Fresh colouration dark grey; inner, dorsal aspect of paired fins charcoal blue.

Description. D I, 7. P I, 9-10. A 16-18. GR (first arch) 10-14, of which 3-5 on upper limb. GR (last arch) 9-13. Vertebrae 50-52 (43-46 free).

Body robust. Head broad, depressed; predorsal profile almost straight, slightly convex at nape. Snout rounded to slightly acute, prominent; lips moderately thick and fleshy, inner margin crenulate. Tiny, fine papilla-like structures on snout and around mouth in all specimens. Mouth very broad, curved, more inferior than sub-terminal; one-quarter to half of upper jaw tooth band exposed when mouth closed. Nostrils rounded, anterior one slightly lateral to posterior one. Eye small, not completely free of head skin, situated dorsolaterally, well to slightly before mid-head length. Gill opening moderately wide, united membrane concave over isthmus, margin broad and free.

Teeth conical, tips sharp or compressed; very slightly depressible; embedded in thick tissue. Five to eight irregular series of teeth in premaxillary band, 4 to 6 in lower band; narrow edentulous space at symphysis of lower jaw. Four tooth patches across front of palate, separated by narrow spaces. Vomerine patches rounded; outer patches large, oval, at least twice as large as vomerine patches. Palate smooth or with few scattered low papillae; two low oblique ridges of epithelial tissue before branchial chamber.

Head shield extensive, very granular, granules low, coarse in large individuals. Ridges of striae flank dorsomedian head groove posteriorly; broader striae extend over supraoccipital process. Groove lanceolate, beginning on snout, extending to base of supraoccipital process; groove flat anteriorly, narrow and deeply excavated posteriorly. Supraoccipital process broad, triangular; sides almost concave; strong median keel. Sides of head slightly venulose; small, oval, naked space in head shield above operculum. Humeral process broad-based, heavily ossified anteroventrally; its triangular shaft extending one-third distance along pectoral fin spine. Axillary pore moderately large.

Barbels flat, thick proximally, thin and wisp-like distally. Maxillary barbel extends to base of pectoral fin or to below dorsal fin base (juveniles). Mandibular barbel reaches pectoral fin base. Mental barbel ends

midway between eye and pectoral fin base. Bases of chin barbels moderately staggered.

Gill rakers well-spaced, half as long as opposing filaments. Numerous, low papillae along back of first two gill arches (fewer in larger fish); no rakers on posterior face of first arch; rarely 1-3 rakers posterodorsally on second arch; 9-10 rakers on posterior face of third arch. Narrow pads of epithelial tissue on gill arches posterodorsally, best developed on second.

Fin spines robust, tips sharp. Outer spine margin with low granules and 1-3 serrae distally; posterior margin with 3-5 serrae (dorsal spine) or 5-10 large antrorse serrae (pectoral). Longest dorsal ray 1.9-2.2 times last ray. Pectoral fin extends to below mid-dorsal fin. Ventral fin short of or reaches anal fin origin (condition in mature females unknown). Adipose fin oblong, long-based, beginning noticeably before anal fin origin, opposite all of anal fin. Anal fin margin concave, longest ray 2.4-3.2 times last ray. Caudal fin moderately short, lobes broad, tapered.

Caudal peduncle moderately deep. Lateral line turned dorsad at tail base, elevated below dorsal fin. Low, short lines of pores diverge from length of lateral line, more abundant anteriorly.

Colour of fresh material. Brown to dusky mauve above, pale yellow or fawn below; iridescent gold on sides. Fins dusky mauve or brown. Barbels pale yellow.

Colour of preserved material. Light brown or tan, paler below; fins brown; barbels fawn. Peritoneum pale.

Comparisons. *Arius hardenbergi* can be distinguished from the similar *Arius proximus* (Ogilby, 1898) by its larger adipose fin (12-19% SL, compared with 6-12% in *A. proximus*), mouth shape, eye diameter (8-12.5% HL, compared with 14-28% in *A. proximus*), extent of head shield, supraoccipital process shape, and swimbladder form (margins smooth versus scalloped in *A. proximus*). The supraoccipital and mouth shapes, paired fin colouration and adipose fin size of *A. hardenbergi* are similar to those of *Cinetodus* (Kailola 1990b). However, the taxa belonging to that genus have rakers along the posterior face of the first two gill arches, different palatal dentition and more restricted gill opening. *Cinetodus carinatus* (Weber, 1913) can be confused with *A. hardenbergi* but *C. carinatus* has more gill rakers on the first gill arch (15-19) and more and stronger serrae along the inner pectoral spine.

Distribution. *New Guinea*: south coast. Vogelkop Peninsula to the Fly River mouth.

Ecology. Muddy, shallow coastal waters and tidal rivers.

Remarks. On a label attached to the largest specimen from Merauke, is written '*Arius uniformis* Hardenberg'. Hardenberg did not publish a description, and there is no unpublished manuscript at the ZMA. This name is therefore not available.

This species probably attains a larger size, although the maximum size specimen I have measured is 254 mm

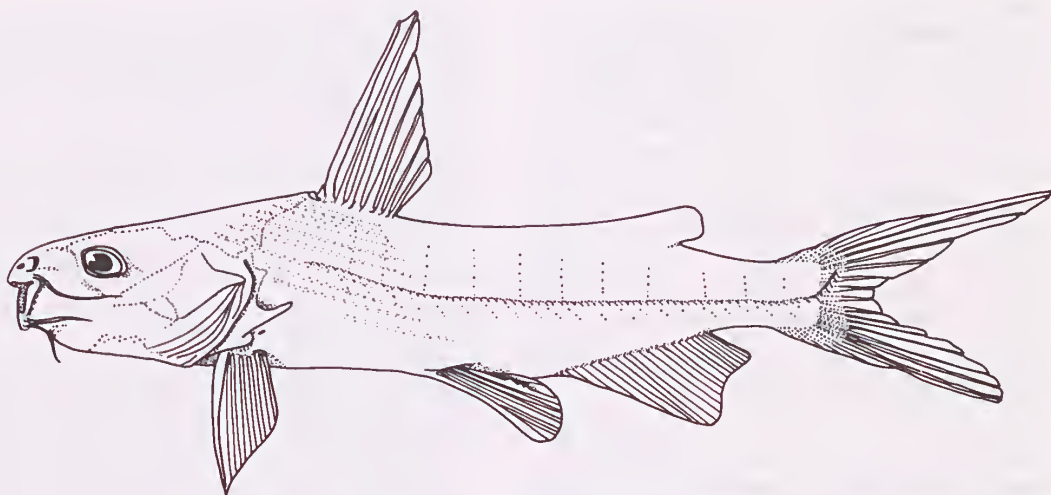


Fig. 9. *Arius hainesi* sp. nov. lateral view, 228 mm SL paratype.

SL. It could have been mistaken in collections for several other species such as *Arius proximus* (Ogilby) and members of the genus *Cinetodus*.

Etymology. I name this species after J.D.F. Hardenberg, not only because he recognised that the species was new but also as an acknowledgement of his insightful contributions to Indo-Australian ichthyology in the mid-twentieth century.

***Arius hainesi* sp. nov.**
(Figs 9-11; Tables 1, 4)

Nedystoma dayi - Tortonese 1964: 24.

Nedystoma dayi (in part) - Kailola 1975: 42.

Nedystoma sp. - Liem and Haines 1977: 25.

Arius species 4 - Kailola 1990b: 459.

Arius sp. 4 - Blaber, Brewer and Salini 1994: 168, fig. 3n.

Type material. HOLOTYPE - NTM S.11507-001, 304 mm SL, Ludmilla Creek (12°27' S, 130°46' E), Darwin, Northern Territory, G. Cole and A. Howard, 19 December 1984. PARATYPES - AMS I.25995-001, 204 mm SL, Baimuru (07°33' S, 144°51' E), Papua New Guinea, A.K. Haines, 12-14 September 1974; QM I.22657, 228 mm SL, Morowan (07°35' S, 144°58' E), Ini Island, Papua New Guinea, A.K. Haines, 15 May 1975; AMS I.27414-001, 237 mm SL, same data, 237 mm SL (cleared and stained); USNM 288553, 135 mm SL, Gulf of Papua (08°00' S, 145°00' E), S. Frusher, 13 July 1981; AMS I.25996-001, 136 mm SL, Gulf of Papua, A.K. Haines, May 1975; CSIRO C.3799, 187 mm SL, Norman River at Karumba (17°29' S, 140°50' E), Queensland, D.J. Turner, 1969; NTM S.10190-002, 2

(88.0-88.2 mm SL), Mickett Creek (12°21' S, 131°00' E), Melville Island, Northern Territory, D. Grey, 26 June 1975 (larger specimen cleared and stained); CSIRO H.4545-01, 2 (120.4-125.9 mm SL), Papua (Irian Jaya) at 4°56.6'S, 137°03.2'E, K. Hortle and A. Haris, 4 September 1996; CSIRO H.4937-03, 222.5 mm SL, Papua (Irian Jaya) at 4°52.1'S, 135°57.7'E, K. Hortle and A. Haris, 6 September 1997; CSIRO H.5252-01, 2 (210-234 mm SL), Papua (Irian Jaya) at 4°53.8'S, 136°54.6'E, K. Hortle and A. Haris, 6 September 1997.

Additional material examined (non type material). KFRS F.O3990, 181.5 mm SL, Murua (07°52' S, 145°47' E), Matupi River, Papua New Guinea, October 1971; KFRS F.O4093, 3 (115-193 mm SL), off Oreke River mouth (08°42' S, 146°29' E), Papua New Guinea, P. Kailola and J. Koaia, 3-4 May 1973; CSIRO H.4958-01, 12 (33-42 mm SL), Papua (Irian Jaya) at 4°52.4'S, 136°57'E, K. Hortle and A. Haris, 1 June 1998 (mouth juveniles); CSIRO H.5174-06, 210 mm SL, Papua (Irian Jaya) at 4°52.6'S, 136°56.5'E, K. Hortle and A. Haris, 6 September 1997; WAM P.29965-002, 94 mm SL, Manimeri River (02°06' S, 133°45' E), Papua (Irian Jaya), G.R. Allen, March 1989; AMS I.27413-001, 2 (108-151 mm SL), Arehava (07°35' S, 144°57' E), Papua New Guinea, A.K. Haines, September 1974.

Diagnosis. Palate without teeth (but autogenous tooth plates present); jaw teeth slender, in short, oblong band. Lips fleshy, thin; mouth small, lower jaw truncate. Barbels thin, short, maxillary barbel reaching only just beyond eye; bases of chin barbels close together. Eye large, 14-24 % HL, lateral. Dorsomedian head groove elongate, deep posteriorly. Gill rakers along posterior

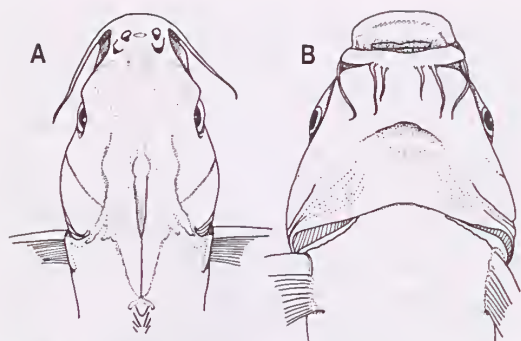


Fig. 10. *Arius hainesi* sp. nov. A, dorsal head view (228 mm SL paratype), B, ventral head view (holotype).

of all arches; gill opening slightly restricted; two large epithelial flaps on palate posteriorly and double folds on upper limb of first two gill arches. A 20-23; total gill rakers (first arch) 32-37. Longitudinal furrows antero-dorsally on body. Fin spines thin, long, slender; adipose fin short-based, over posterior two-thirds of anal; ventral fin pad of sexually mature females scalloped and tapered. Fresh colouration dark grey above and iridescent purple; palate and branchial chamber often purplish brown to charcoal.

Description. D 1.7, P 1, 8-11. A 20-23. GR (first arch) 32-37, of which 10-12 on upper limb. GR (last arch) 31-37. Vertebrae 49-50 (43-44 free).

Body moderately elongate, cylindrical; head slightly depressed. Predorsal profile straight, abruptly convex at nape. Snout slightly rounded or truncate, curved ventrad, overhanging subinferior mouth. Lips thin, fleshy or 'rubbery', inner aspect spongy and papillose. Mouth gape moderately wide, lower jaw truncate or horizontal; all of premaxillary tooth band visible when mouth closed. Nostrils large, rounded, anterior nostril slightly median to posterior one. Shallow groove usually present on snout between posterior nostrils. Eye large, rounded,

prominent, situated laterally at or slightly before mid-head length, margin free of head skin; lateral ethmoid prominent before eye. Gill openings somewhat restricted ventrally, membranes attached broadly to isthmus, margin concave.

Teeth in jaws slender, long, depressible; very fine; embedded in tissue; in 5-6 series. Tooth band (both jaws) interrupted at symphyses by edentulous space. Pre-maxillary bands elongate-oval. No teeth on palate. Palate almost smooth or with low, scattered papillae. One large pair of epithelial tissue folds hangs from palate into anterior part of branchial chamber.

Head shield rugose or finely granular. Granules conspicuous, usually sharp, arranged in series along dorsomedian head groove and along edge of shield in larger specimens. Dorsomedian groove begins at level of nostrils and continues to supraoccipital process base; groove flat anteriorly, thence deeply excavated; conspicuous. Rugose supraoccipital process triangular with straight sides; sharp median keel prominent. Naked space in head shield above gill opening. Large venules on sides of head. Lateral head skin and 'shoulder' skin develop 7-10 longitudinal furrows or ridges with age; most apparent in individuals longer than about 150 mm SL. Humeral process triangular, indented above, heavily ossified anteroventrally, shaft oblique, acute; granules arranged in series along process. Moderate sized, slit-like axillary pore present.

Barbels thin, rounded proximally, flattened and wisp-like distally. Maxillary barbel reaches to eye or halfway between eye and gill opening (juveniles); mandibular barbel extends to below middle of eye; mental barbel not or just reaches front eye margin. Chin barbel bases close together, almost transversely aligned.

Gill rakers long, equal to gill filament length. Shorter rakers along posterior face of all arches: 32-36 along first arch, 33-40 on second, 30-34 on third. Curious large double fold (or pouch) of epithelial tissue links upper limb of first two arches.

Fin spines long, slender, rather compressed; sides smooth to finely striate; anterior border with sharp granules or ridges. Low serrae along distal part of dorsal fin spine hind border and 25-35 sharp, large retrorse serrae along pectoral fin spine hind border. Last dorsal fin ray 3.0-3.7 times in longest ray. Pectoral fin reaches just beyond dorsal fin. Ventral fin narrow in males, reaching second or third anal fin ray; broad in females, extending to about fifth anal fin ray; mature females with curiously-shaped thickening along dorsal aspect of sixth ray consisting of series of lobes and proximally a short, lateral horizontal process (Fig. 11C). Adipose fin short-based, oblong; above middle of anal fin. Outer margin of anal fin truncate (adult) to deeply concave (juveniles), last ray 2.8-3.2 times in longest ray. Caudal fin lobes narrow, tapered, upper lobe slightly the longer.

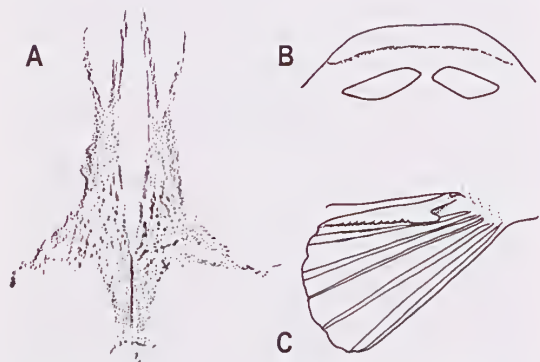


Fig. 11. *Arius hainesi* sp. nov. A, rubbing of head shield (228 mm SL paratype), B, arrangement of upper tooth patches (204 mm SL paratype), C, ventral fin of mature female showing pad of epithelial tissue.

Caudal peduncle moderately deep. Lateral line elevated below dorsal fin, curved dorsad at tail base. Thin, dorsally-directed branchlets of lateral line conspicuous; vertical series of fine pores diverging from lateral line extend over upper body surface.

Colour of fresh material. Iridescent charcoal-purple on head and back, otherwise dark grey or brown above, white below. Sharp division between dorsal and ventral colours. Fins pale. Lining of mouth and branchial chamber either white to cream, or purplish brown to charcoal.

Colour of preserved material. Dark brown or charcoal grey over upper two-thirds of head and body, pale orange-fawn or dusky grey below. Both lips pale. Dorsal, adipose and caudal fins dusky tan with broad, brown margins. Upper aspect of pectoral fin dark grey or brown; upper ventral fin, anterior anal fin rays and anal fin margin dusky. Palate and branchial chamber pale to dark brown or charcoal. Barbels brown.

Comparisons. *Arius hainesi* superficially resembles *Nedystoma dayi* (Ramsay and Ogilby, 1886) in having a toothless palate, epithelial folds around and before the anterior gill arches, and many gill rakers. However, the

shapes of the posterior head groove and mature female ventral fin, the short barbels (maxillary barbel 29-56 % HL, compared with 46-76 % HL in *N. dayi*), longer snout (38-43 % HL, compared with 30-36 % HL in *N. dayi*) are among distinguishing characters. The two species also apparently occupy different habitats (*N. dayi* is almost strictly freshwater). Tortonese's (1964) '*Nedystoma dayi*' from Katau (09°08' S, 142°56' E) must be referable to this species.

Distribution. *New Guinea*: southern coast from Kamora to Otokwa rivers (Papua (Irian Jaya)) and from Katau (west of Fly River delta) to Aird Hills and Oreke River (Papua New Guinea); possibly continuous distribution and more extensive westwards. *Australia*: from vicinity of Darwin to the southern Gulf of Carpentaria.

Ecology. Predominantly in marine waters of the lower estuaries, along the coast and off river mouths. In Papua New Guinea the species is common locally (such as the Era River - Morowan area) (Haines 1979) although in central-southern Papua (Irian Jaya), *A. hainesi* is common in the estuaries.

Remarks. *Arius hainesi* attains a maximum size of 320 mm FL (Papua (Irian Jaya) material).

Etymology. Named for Alan K. Haines, who worked in fisheries in Papua New Guinea between 1972 and 1976. He undertook several surveys of river systems entering the Gulf of Papua (notably the Purari) and developed a sound appreciation of those river systems and their aquatic fauna. Through his ability to distinguish the species and his faithful recording of the biology and ecology of the fork-tailed catfishes in the Gulf rivers, Alan made a significant contribution to our knowledge of this fish family in the Australian and New Guinea region.

Arius paucus sp. nov.

(Figs 12-13; Table 5)

Arius midgleyi Kailola and Pierce, 1988: 75 (in part).

Type material. HOLOTYPE - QM I.12910, 326 mm SL, Flinders River near Maxwellton (20°47' S, 142°43' E), Queensland, H. and M. Midgley, 14 October 1974 (paratype of *Arius midgleyi*). PARATYPES - QM I.12757, 310 mm SL, Flinders River near Maxwellton, H. and M. Midgley, 14 October 1974 (paratype of *Arius midgleyi*); QM I.16730, 2 (315-329 mm SL), Flinders River near Maxwellton, H. and M. Midgley, October 1974 (paratypes of *Arius midgleyi*); QM I.11364, 205 mm SL, Forest Home Station (18°15' S, 143°02' E), Gilbert River, Queensland, T.C. Marshall, 24 September 1953 (paratype of *Arius midgleyi*); AMS I.25315-001 (previously IB.3159/2882), 171 mm SL, same data (paratype of *Arius midgleyi*); QM I.11990, 145.5 mm SL, Mitchell River (16°00' S, 142°20' E), Queensland, 8 September 1959, (paratype of *Arius midgleyi*); QM I.16735, 240 mm SL, Hodgson River (14°54' S, 134°33' E), Northern Territory, H. and M. Midgley, 17 September

Table 4. Percent of head length (HL) and standard length (SL) for *Arius hainesi* sp. nov. n = sample size; \bar{x} = mean; SD = standard deviation.

Character	holotype	n	<i>Arius hainesi</i> range	\bar{x}	SD
Percent of HL					
head height	54.8	14	45.6 - 65.1	55.2	5.5
head width	68.1	14	52.3 - 74.6	66.4	5.7
eye diameter	14.1	14	14.1 - 23.8	18.7	2.5
mouth gape	34.0	14	27.5 - 37.9	32.2	2.8
internostil distance	18.4	14	15.6 - 19.1	18.2	0.9
snout length	43.3	14	38.2 - 43.3	40.6	1.7
longest barbel length	34.2	14	28.9 - 55.8	42.1	7.7
bony interorbital width	28.0	14	27.0 - 42.6	30.1	3.7
occipital proc. length	28.0	14	22.9 - 50.0	30.3	6.6
occipital proc. width	12.1	14	12.1 - 20.5	16.6	2.3
Percent of SL					
HL	32.1	14	27.7 - 33.0	30.4	1.9
head height	17.6	14	15.0 - 18.4	16.7	1.2
head width	21.9	14	17.3 - 21.9	20.1	1.4
eye diameter	4.5	14	4.5 - 6.6	5.7	0.6
mouth gape	10.9	14	8.4 - 12.1	9.8	1.1
internostil distance	5.9	14	4.9 - 6.0	5.5	0.4
snout length	13.9	14	10.8 - 13.9	12.4	1.1
longest barbel length	11.0	14	9.5 - 15.8	12.7	1.9
bony interorbital width	9.0	14	8.0 - 12.8	9.2	1.2
occipital proc. length	9.0	14	7.5 - 13.9	9.1	1.5
predorsal length	40.8	14	36.5 - 42.2	39.6	1.6
length dorsal f. base	11.6	14	9.9 - 12.3	11.2	0.6
interdorsal length	28.1	14	25.9 - 31.0	28.8	1.5
length adipose f. base	6.2	14	4.5 - 9.4	6.7	1.4
length anal f. base	17.0	14	17.0 - 19.9	18.5	1.0
caudal ped. depth	8.3	14	7.1 - 8.5	7.9	0.4
caudal ped. length	15.4	14	13.9 - 17.6	15.8	1.1
pectoral spine length	23.0	11	19.2 - 25.1	22.7	2.0
dorsal spine length	23.4	11	21.4 - 26.4	23.9	1.4

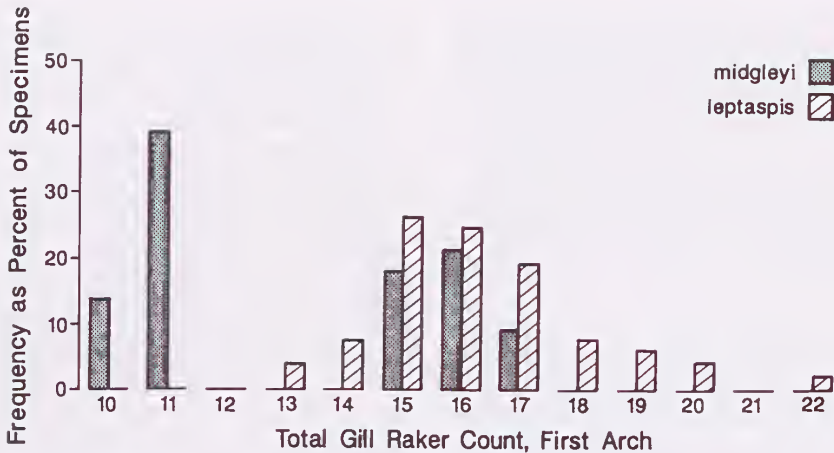


Fig. 12. Range of total gill raker count (first arch) of *Arius midgleyi* and *A. paucus* sp. nov. (species combined) and 57 specimens of *Arius leptaspis* (Bleeker) from northern Australia and southern New Guinea. *Arius paucus* sp. nov. counts are at the left of the figure.

1979 (paratype of *Arius midgleyi*); QM I.16738, 2 (327 mm SL and 151.5 mm HL), Mannaburoo Hole (16°05' S, 135°22' E), Limmen Bight River, Northern Territory, H. and M. Midgley, 29-30 August 1979 (paratypes of *Arius midgleyi*); NTM S.12070-001, 2 (298-315 mm SL), same data (paratypes of *Arius midgleyi*); QM I.16737, 310 mm SL, same locality, H. and M. Midgley, 1 September 1979 (paratype of *Arius midgleyi*); NTM S.12083-001, 331 mm SL, Wilton River (13°46' S, 134°28' E), H. and M. Midgley, 25-27 September 1979 (paratype of *Arius midgleyi*); NTM S.1775, 257 mm SL, Wollongorang Station (17°13' S, 137°57' E), Northern Territory, D. Howe, 15 June 1974 (paratype of *Arius midgleyi*); CAM F.36, 273 mm SL, same data (paratype of *Arius midgleyi*).

Additional material (non-type). QM I.16741, 2 (123.5-131 mm HL), McArthur River (24°46' S, 143°44' E), Queensland, H. and M. Midgley, June 1975; NTM S.12077-001, 107.5 mm HL, Roper River (14°46' S, 134°01' E), Northern Territory, H. and M. Midgley, September 1979; NTM S.11153-001, 110 mm HL, Mainoru River (14°01' S, 134°03' E), Northern Territory, H. and M. Midgley, September 1979.

Diagnosis. Gill rakers total 10-11 on first gill arch, 11-14 on last arch. Eye diameter as percentage of head length 9-15. In addition, the characters of *Arius midgleyi* Kailola and Pierce: sleek body; strong jaws; jaws upturned slightly at symphyses, mouth broad; snout truncate in profile; head oblong, its width averaging 66% HL. Supraoccipital process narrow with parallel margins. Numerous fine, sharp teeth on palate in transverse band of four oblong groups. No rakers on posterior aspect of gill arches. A 16-19; vertebrae 20+7-8+28-29. Barbels thin and short, rarely reaching beyond pectoral fin base and less than 25% SL.

Comparisons. *Arius paucus* differs from *A. midgleyi* in gill raker numbers (10-11 on first arch in *A. paucus*,

versus 15-17 on first arch in *A. midgleyi*) and eye size (8.9-15.3% HL in *A. paucus* versus 12.9-21.8 % HL in *A. midgleyi*) (Table 5). No other morphometric characters distinguish these species, although juvenile colouration may be important.

Furthermore, there is a clear disjunction in range of the two species: *A. midgleyi* distributed in the west (the Victoria, Katherine, Daly, Ord, remaining Kimberley and northern river systems including the Alligator); and *A. paucus* distributed in the east (the Roper and Flinders River systems and all other rivers draining into the Gulf of Carpentaria).

Distribution. River systems of the Roper (Limmen Bight, Roper, Hodgson, Wilton and Mainoru), McArthur, Tooganginie Creek, Robertson and Calvert (rare); south-east to the Flinders, Gilbert, Staaten and Edward River systems (Strathgorden Lagoon) on Cape York Peninsula (Midgley 1979, 1980, 1981, 1982, 1983, 1984, pers. comm.).

Remarks. *Arius paucus* and *A. midgleyi* are most closely related to *Arius leptaspis* (Bleeker) and less so, to *Arius latirostris* Macleay, a Papuan endemic. The distinguishing features of these four taxa were described

Table 5. Comparison of key characters between *Arius paucus* sp. nov. and *A. midgleyi*. n = number; \bar{x} = mean; SD = standard deviation; GR 1 = rakers on first gill arch; GR 4 = rakers on last gill arch.

Species	variable	Eye diam. % HL	Total GR 1	Total GR 4
<i>A. midgleyi</i>	holotype	13.3	16	18
	range, n = 14	12.9 - 21.8	15-17	16-19
	\bar{x}	17.1	15.8	17.3
	SD	3.2	0.7	0.9
<i>A. paucus</i>	holotype	9.1	11	13
	range, n = 16	8.9 - 15.3	10-11	11-14
	\bar{x}	11.0	10.7	12.8
	SD	1.7	0.5	0.8

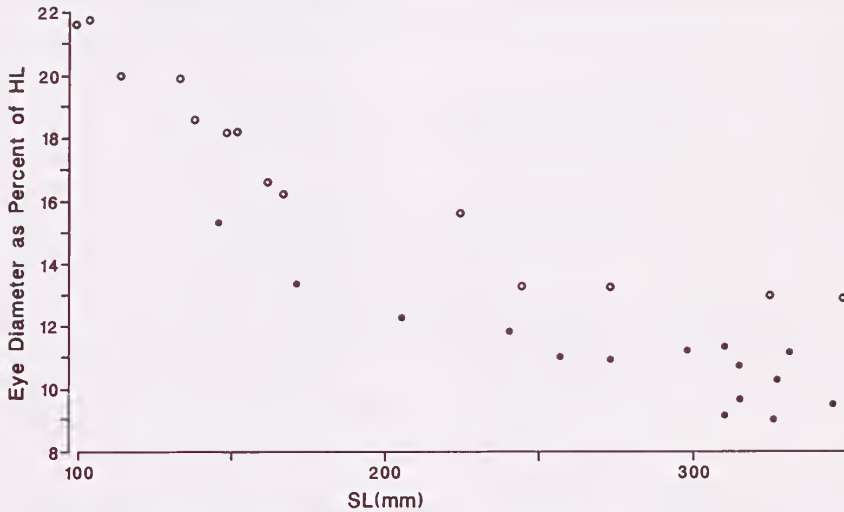


Fig. 13. Comparison of eye size between *Arius midgleyi* (hollow circles) and *A. paucus* sp. nov. (solid circles).

by Kailola and Pierce (1988). *Arius paucus* and *A. midgleyi* are common and widespread in river systems of northern Australia, and attain a large size (to about 28 kg and 1.3 m total length: *A. midgleyi*) (Kailola 1990b).

Etymology. From the Latin, *paucus*, meaning few, or less. Refers to the new species having fewer gill rakers and a smaller eye than does *A. midgleyi*.

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Two new genera and three new species of Thylacinidae (Marsupialia) from the Miocene of the Northern Territory, Australia

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ABSTRACT

Three new species and two new genera of Thylacinidae from the Northern Territory of Australia bring the total number of known mid and late Tertiary species to 11 in eight genera. *Tyarrpecinus rothi* gen. et sp. nov. from the Alcoota Local Fauna (Waite Formation), and *Nimbacinus richi* sp. nov. and *Mutpuracinus archibaldi* gen. et sp. nov. from the Bullock Creek Local Fauna (Camfield Beds), are relatively small and amongst the more plesiomorphic members of the family. Phylogeny reconstruction using cladistic methods and biochronological data indicate that a major radiation occurred within the family in pre-Miocene times. Specialisation in the form of dental carnassialisation appears to have evolved in parallel in at least two crown groups, one of which includes the recently extinct 'Tasmanian wolf', *Thylacinus cynocephalus*. The other, together with all the lineages represented by unspecialised species, apparently did not survive into the late Miocene. However, insufficient data are available to show what the regional, let alone continental, pattern of succession was during the Miocene.

KEYWORDS. Marsupialia, Thylacinidae, *Mutpuracinus archibaldi* gen. et sp. nov., *Tyarrpecinus rothi* gen. et sp. nov., *Nimbacinus richi* sp. nov., Alcoota Local Fauna, Bullock Creek Local Fauna, Camfield Beds, Waite Formation, phylogeny, evolution, Miocene, Australia.

INTRODUCTION

The Thylacinidae is a family of dasyuromorphian marsupials, the last member of which, the Tasmanian wolf (*Thylacinus cynocephalus* (Harris)), was extinguished by bounty hunters in the 1930s. Pliocene and Pleistocene fossil species have all been synonymised with *T. cynocephalus* (Dawson 1982), and the fossil record of the family was only extended into the late Miocene with the discovery at Alcoota of *Thylacinus potens* Woodburne, 1967. *Thylacinus potens* provided the first indication that thylacinids were a radiated family, as the species is derived dentally in ways that precludes its direct ancestry of *T. cynocephalus*. In more recent years, the fossil record has been greatly expanded by new discoveries at Alcoota, Bullock Creek and Riversleigh (Fig. 1), spanning the ?late Oligocene to late Miocene (Muirhead and Archer 1990; Wroe 1996; Muirhead 1997; Murray 1997; Muirhead and Wroe 1998). On the basis of the known diversity of thylacinids in the central and northern Australian deposits, it might be anticipated that similar diversity will eventually be found in correlative deposits in the Lake Eyre and

Tarkarooloo Basins of South Australia. So far, only a single premolar of unknown affinity has been listed from Lake Ngapakaldi, South Australia (Kutjamarpu Local Fauna, Wipijiri Formation of the Lake Eyre Basin) (Archer 1982). Hypotheses of phylogeny within the family are currently in a state of flux as each new discovery adds to the diversity of fossil forms available for analysis.

Tyarrpecinus rothi gen. et sp. nov. (Alcoota LF, late Miocene), *Mutpuracinus archibaldi* gen. et sp. nov. and *Nimbacinus richi* sp. nov. (both Bullock Creek LF, mid Miocene) represent three new species and two new genera of Thylacinidae, and raise the total number of known Tertiary species to 11 in eight genera. The new species are comparatively small members of the family (small and medium-dog sized, compared to the wolf-sized *T. cynocephalus*, for example). Cladistic analysis of dental characters resolves them as plesiomorphic members of the family, closely related to certain previously described forms (Muirhead 1992, 1997; Wroe 1996; Muirhead and Wroe 1998). Excellent preservation of the maxilla of *Mutpuracinus* and a complete dentary of *Nimbacinus richi* sp. nov. fill some important gaps in



Fig. 1. ?Late Oligocene and Miocene localities that have produced thylacines.

our knowledge of Tertiary thylacinid morphology. The three new species and other recently reported late Oligocene and Miocene finds exemplify a gradual structural succession towards the genus *Thylacinus*.

The current consensus is that thylacinids are dasyuromorphians derived from a dasyurid ancestor, although a possible affinity with South American borhyaenoids was a matter of prolonged debate from 1903 into the 1980s (e.g. references in Archer 1982; Muirhead and Wroe 1998). We accept argument presented by Wroe (1996) and Muirhead and Wroe (1998) for the inclusion of *Muribacinus gadiyuli* Wroe, 1996, and *Badjcinus turnbulli* Muirhead and Wroe, 1998, in the Thylacinidae (rather than in the Dasyuridae), and offer no additional observations on the issue regarding the thylacinid status of the similarly plesiomorphic *Mutpuracinus archibaldi* gen. et sp. nov. Other than to remark on the assumption that the metaconid reduces uniformly along the tooth row in thylacinids, we support the re-diagnosis of the family presented in Muirhead and Wroe (1998).

METHODS

Adult dental terminology (Flower-Luckett) recognises P1-3, M1-4 (Flower 1869, Luckett 1993); all Archer (1978, 1982) terminology in cited literature has been converted. Specimens are Northern Territory Museum (NTM) Palaeontological collection unless designated QMF (Queensland Museum, Fossil collection). The thylacinid-producing formations referred to are not precisely dated, and their ages can at present only be loosely expressed in terms of the standard geological timescale. Consequently, modifiers such as 'early' and 'late' are left uncapitalised when attached to the standard

Tertiary epochs so as not to imply a geochronological precision that does not exist. Stage-of-evolution biochronological concepts and terminology follow Megirian (1994).

Key to anatomical abbreviations.

A-E	Stylar cusps
AC	Anterior cingulum or precingulum
ALV	Alveolus
ANP	Angular process
CCR	Centrocrista
CON	Condyle
CRN	Reception notch for canine
END	Entoconid
HLD	Hypoconulid
HYD	Hypoconid
IFO	Incisive foramen
IOF	Infraorbital foramen
MAF	Mandibular foramen
MCL	Metaconule
MCR	Submasseteric crest
MEC	Metacone
MED	Metaconid
MEF	Mental foramen
MFO	Masseteric fossa
MJS	Maxillo-jugal suture
PAC	Paracone
PAD	Paraconid
PAF	Palatal fenestra
PCD	Precingulid
PCL	Protoconule
PMF	Posterior mental foramen
PMS	Premaxillo-maxillary suture
PRC	Protocone
PRD	Protoconid
PSD	Parastylid

SYSTEMATIC PALAEOLOGY

Order Dasyuromorphia Gill, 1872
 Superfamily Dasyuroidea Goldfuss, 1820
 Family Thylacinidae Bonaparte, 1838
Mutpuracinus gen. nov.

Type species. *Mutpuracinus archibaldi* sp. nov. by monotypy.

Diagnosis. Small thylacinid with strong expression of stylar cusps on M¹⁻³; large, posteriorly directed P³; infraorbital foramen not in contact with jugal and situated over posterior root of M¹. Size similar to holotype of *Muribacinus gadiyuli* (QMF30386); lower position of zygomatic root, more anterior position of infraorbital foramen relative to the teeth (i.e. over anterior root of M¹); more posteriorly-directed premolar crowns; larger posterolingual cuspule on P³; M² narrower relative to length; larger stylar cusp D on M¹⁻³ and presence of stylar

cuspid C and E on M^{1-2} ; paracone more reduced relative to metacone on M^{1-2} ; M_4 metaconid more reduced; narrower cingulids and talonids on lower molars. Differs from *Badjcinus turnbulli* in which the jugal closely approaches the infraorbital foramen opening above P^3 ; the upper premolar crowns are more slender, taller; M^1 lacks stylar cusps on anterior lobe, preparacrista parallel to long axis of tooth row and M^3 with minute stylar cusp D. Differs from *Nimbacinus dicksoni* Muirhead and Archer, 1990, which is significantly larger; the infraorbital foramen is within the jugal and situated over anterior root of M^2 ; in which conules are more strongly expressed and M^2 distinctly longer than M^3 . Differs from *Wabulacinus ridei* Muirhead, 1997, *Ngamalacinus timmulvaneyi* Muirhead, 1997, and species of *Thylacinus* in showing less reduction of metaconids on $M_{2,4}$; absence of carnassial notch in cristid obliqua and less reduction of entoconid and protocone.

Etymology. *Mutpura* is the tribal designation of the Aboriginal people living in the Camfield district [= *Tjambutjambulani* - Tindale 1974] + *kynos* (Gr.) 'dog'.

***Mutpuracinus archibaldi* sp. nov.**

(Figs 2-4, Table 1)

Diagnosis. As for genus.

Type material. HOLOTYPE - NTM P907-3 (Blast Site), left maxilla with P^2 - M^4 , missing canine and P^1 . PARATYPE - NTM P9612-5 (Top Site), left dentary fragment with $M_{3,4}$, missing ascending ramus and anterior part of horizontal ramus.

Referred material. All NTM: P9464-120 (Top Site), right premaxilla with I^{1-4} alveoli; P9464-119 (Top Site) posterior fragment of horizontal ramus of right dentary preserving submasseteric crest, part of condyle and part of angular process; P87108-10 (Blast Site), isolated right M_4 .

Type locality. 'Blast Site', Bullock Creek, Northern Territory, Australia. Low limestone hill 1 km east of type section of Camfield Beds; $131^\circ 31'E$, $17^\circ 07'S$; Wave Hill 1:250 000 Map Sheet. SE/52-8.

Lithic unit, fauna and age. Camfield Beds, Bullock Creek Local Fauna, middle Miocene on the basis of marsupial stage-of-evolution biochronology (Woodburne *et al.* 1985; Murray *et al.* 2000). Both fossil quarries (sites) listed above are in the vicinity of the type locality (Murray and Megirian 1992: fig. 2).

Description. *Premaxilla* (Fig. 2A,B). Edentulous, 13.0 mm anteroposteriorly by 11.5 mm dorsoventrally, right premaxillary fragment P9464-120 is missing the ascending process. Four incisor alveoli are present: I^1 is largest; I^{2-3} are narrower; and I^4 is slightly smaller than I^1 but larger than I^{2-3} . The incisor arcade is nearly straight and less acutely angled relative to the midline than in *Dasyurus hallucatus* (Dasyuridae), for example. A large reception socket for the lower canine measures 4.5 mm anteroposteriorly by 6.5 mm dorsoventrally. The anterior margin of the right incisive foramen indicates a narrow, slot-like structure.

Maxilla (Fig. 3A,B). P907-3 preserves alveoli for upper canine and P^1 and remainder of left cheek tooth

Table 1. Measurements (mm) of cheek teeth. L = length; W = width; AW = anterior width; PW = posterior width.

<i>Mupuracinus archibaldi</i> gen. et sp. nov.						lower cheek teeth													
P_1		P_2		P_3		M_1			M_2			M_3			M_4				
L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	
P9612-5	-	-	-	-	-	-	-	-	-	-	-	-	5.7	3.6	2.9	5.9	3.3	2.3	
P87108-10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.3	2.9	2.2	
upper cheek teeth																			
P^1		P^2		P^3		M^1			M^2			M^3			M^4				
L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	
P907-3	-	-	4.5	1.8	5.5	2.4	3.0	5.8	4.1	6.2	5.7	5.0	6.5	5.4	5.7	7.0	6.0	4.7	3.5
<i>Nimbacinus richi</i> sp. nov.						lower cheek teeth													
P_1		P_2		P_3		M_1			M_2			M_3			M_4				
L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	
P9612-4	5.0	2.0	6.1	2.8	7.2	2.1	3.1	7.0	3.3	4.2	8.3	4.5	4.4	8.2	5.0	4.0	8.7	4.2	2.5
P8695-92	-	-	5.8	2.8	-	-	-	6.2	2.9	3.2	-	-	-	-	4.3	3.6	7.2	-	3.0
P904-7	-	-	-	-	-	-	-	-	-	-	7.4	4.1	4.3	8.0	4.5	4.1	7.9	4.1	2.9
P85553-3	4.5	1.7	6.0	2.8	-	-	-	6.9	-	4.0	-	-	-	-	-	-	-	-	-
<i>Tyarrpecinus rothi</i> gen. et sp. nov.						upper cheek teeth													
P^1		P^2		P^3		M^1			M^2			M^3			M^4				
L	W	L	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	
P98211	-	-	6.5	2.5	-	-	-	4.8	7.0	7.3	-	-	-	7.7	7.9	9.8	-	-	-

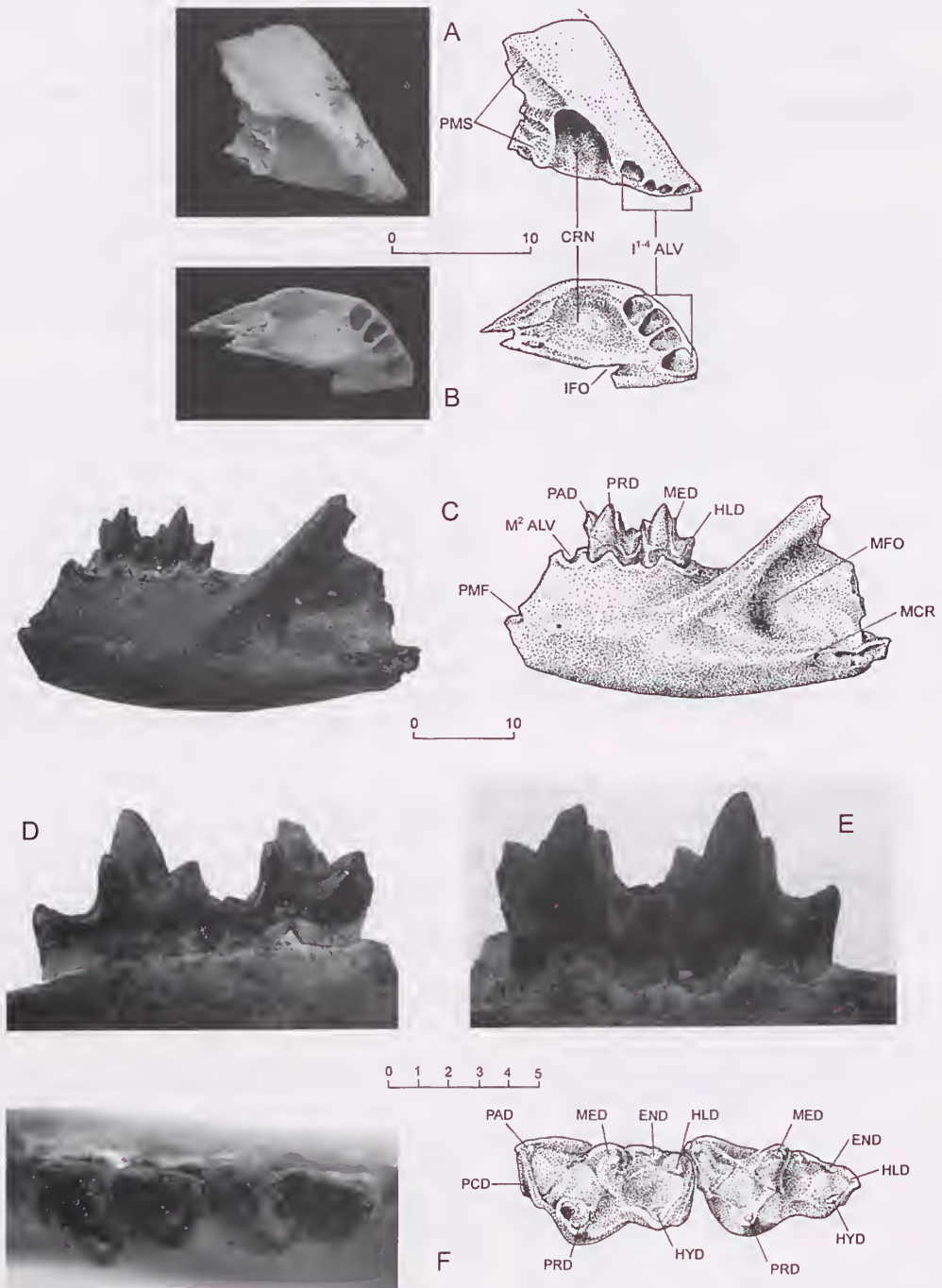


Fig. 2. *Mutpuracinus archibaldi* gen. et sp. nov. Referred right premaxilla (P9464-120) in A, lateral, and B, occlusal views. Paratype left dentary fragment (P9612-5) in C, lateral view; D, medial, E, lateral and F, occlusal, views of molars M_{3,4}. Scale bars in mm.

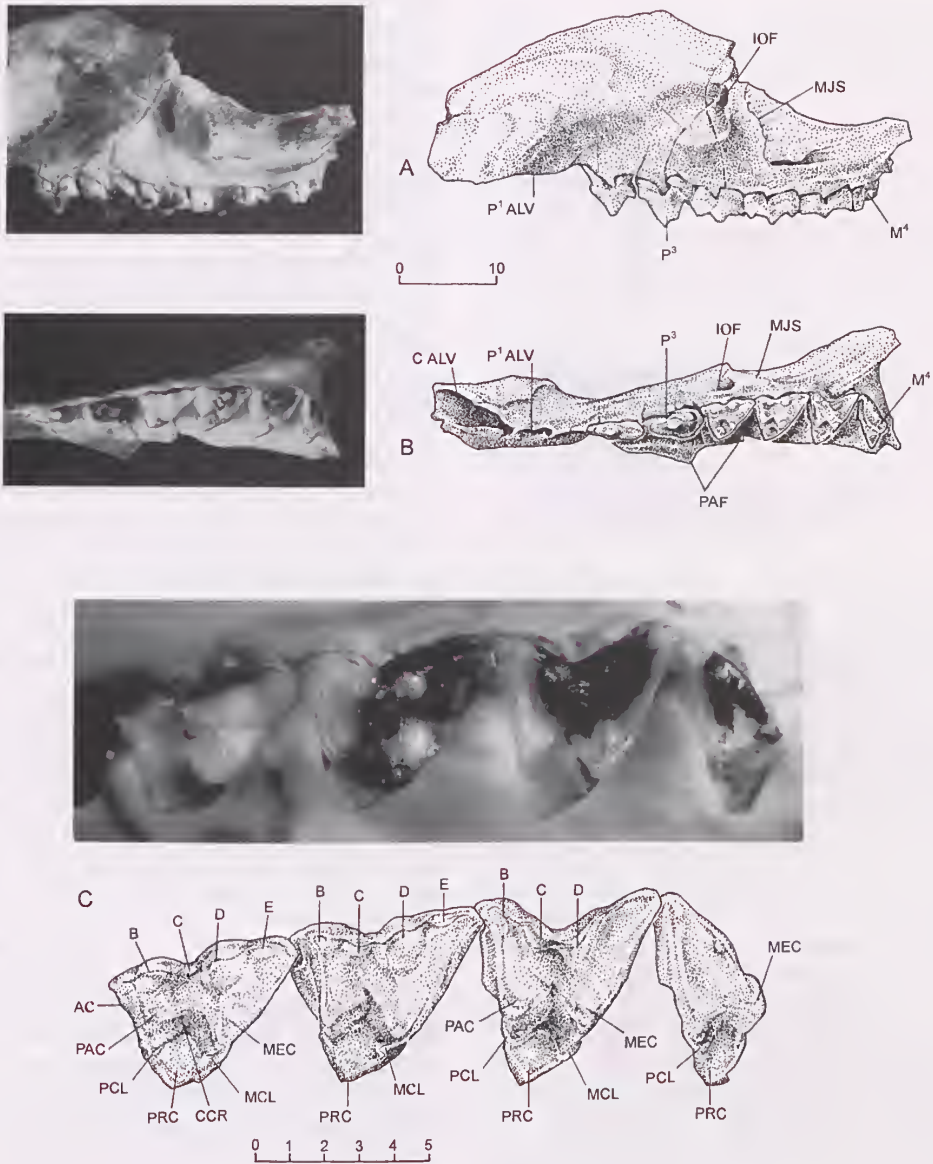


Fig. 3. *Mutpuracinus archibaldi* gen. et sp. nov. holotype left maxilla (P907-3) in: **A**, lateral view; **B**, occlusal view; and **C**, detailed occlusal view of molars M^1 - M^4 . Scale bars in mm.

row; premaxillary contact preserved anterodorsally and nasal contact preserved dorsally; posterior (lacrimal) process missing; jugal process intact. Canine alveolus planoconvex, about 3.5 mm wide by 5.5 mm antero-posteriorly. Alveolus for P^1 situated immediately posterior to the canine alveolus, about 3.5 mm long, oriented slightly obliquely to succeeding premolars. A diastema 4.0 mm long separates P^1 from P^2 . Crown of P^2 4.6 mm long, separated from P^3 by narrow, but distinct, slot that, while only 0.7 mm wide, is suggestive of

rudimentary diastema. P^3 much larger than P^2 with crown projecting well below occlusal line of the other cheek teeth. Labial margin of molar row gently arcuate. Interdental embrasures present between M^1 - M^3 , becoming increasingly larger and distinct posteriorly. Anterior margin of posterior palatal fenestra preserved at the level of P^3/M^1 . Palatal processes thin posteriorly, thickening anteriorly in front of fenestral margin towards P^3 . Jugal contact a shallow, crescentic depression extending to within about 2.5 mm of infraorbital foramen dorsally

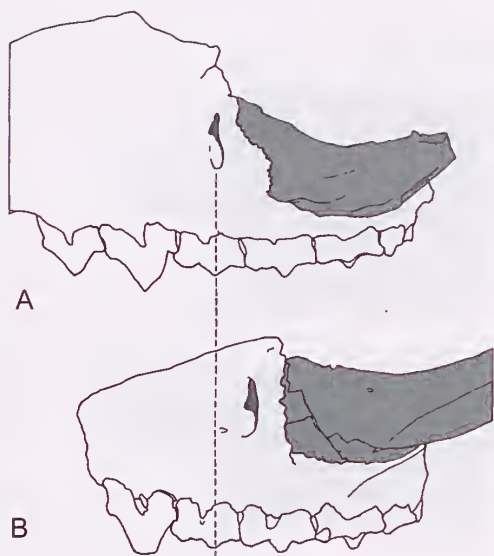


Fig. 4. Comparison of maxillae of A, *Mutpuracinus archibaldi* gen. et sp. nov. and B, *Muribacinus gadiyuli* drawn to the same scale, showing differences in the position of the infraorbital foramen relative to M^1 . (B reversed: after Wroe 1996: fig. 1.)

and about 4.0 mm ventrally. Infraorbital foramen large, about 5.0 mm vertically and 2.5 mm mediolaterally (Fig. 4), opening behind well-defined circular infraorbital fossa, about 12 mm in diameter. The posterior margin of the foramen is aligned with the distal root of M^1 . A shallow depression extending anterodorsally from infraorbital fossa is bounded dorsally by very distinct, sinuous groove terminating about 12 mm above level of canine alveolus. External surface of the canine alveolus bulges conspicuously outwards from surrounding contours of maxilla, resulting in a wide concavity in the vertical profile of specimen. Lateral surface of alveolar bulge rugose, with sharply defined posterior crest.

Incisors, I^{1-4} . Alveoli only (Fig. 2A,B): I^1 largest, broadly oval, 2.0 mm wide, 2.1 mm anteroposteriorly; I^2 triangular, 1.5 mm wide, 1.8 mm long, slightly wider than I^3 ; I^3 narrow, slot-like; 1.3 mm wide, 2.1 mm long; I^4 , ovo-triangular, 1.8 mm wide, 2.0 mm anteroposteriorly.

Canine. Alveolus only (Fig. 2A,B), 5.5 mm anteroposteriorly; 3.5 mm mediolaterally; planoconvex shape; root socket 14.0 mm deep, angled $\sim 30^\circ$ to palatal plane.

Premolar, P^1 (Fig. 3A,B). Alveolus only, 3.5 mm anteroposteriorly, anterior root socket 1.3 mm diameter; angled about 12° from plane of P^{2-3} .

P^2 (Fig. 3A,B). Crown 4.5 mm long, 1.8 mm maximum width; low anterior basal crest, concave anterior margin, tip directed posteriorly; slight posterolingual expansion and small posterobasal cusps; posterior root larger than anterior.

P^3 (Fig. 3A,B). Much larger than P^2 , 5.5 mm anteroposteriorly by 3.0 mm posterior width; low anterobasal crest; concave, rounded anterior margin, tip directed posteriorly; convex, crested posterior margin; low, well-developed posterolingual cusps developed on thick basal cingulum, terminating in elevated postero-medial cusps; posterolabial cingulum poorly developed.

Molar, M^1 (Fig. 3C). Paracone situated much more labially than metacone, very short transverse preparacrista; centrocrista nearly parallel to axis of tooth row; metacone large, premetacrista nearly transverse. Talon broad anteroposteriorly and short transversely; small metaconule and protoconule present; protocone large. Styler cusp B closely adpressed to paracone; higher but slightly smaller than the latter; vestigial styler cusp C situated at base of styler cusp D, a large conical cusps occupying about half the posterior lobe of the crown. Well-developed ectoflexus present, buccal occlusal profile of crown distinctly lobate. Low swelling in the position of styler cusp E (heavily worn); weak precingulum present with shallow interproximal notch for P^3 .

M^2 (Fig. 3C). Larger, more equi-triangular crown; paracone extends much further lingually than in M^1 ; short, transverse preparacrista extends to styler cusp B; styler cusp C well-developed, about equal in size to B; styler cusp D large, conical, occupies slightly less than half of metastylar lobe of crown, slightly smaller but nearly equal in height to metacone; small, distinct styler cusp E situated midway between D and metastylar tip. Metacone much larger than paracone. Talon broad, but more V-shaped than in M^1 , conules small, protocone narrow. Prectingulum well-developed with notch for metastyle of M^1 .

M^3 (Fig. 3C). Larger than M^2 in occlusal aspect, significantly wider transversely, equal in length labially and slightly longer posterolingually; styler cusp B reduced; styler cusp C well-developed but low; styler cusp D large, triangular, but considerably reduced in height and transverse width; tiny cusps present in position of styler cusp E. Ectoflexus strong, parastylar and metastylar tips slender, lobate. Preparacrista long, straight, transverse; paracone less reduced relative to metacone; postmetacrista longer than in M^2 . Talon narrow, distinctly V-shaped, small conules present, more distinct than in M^2 ; protocone reduced. Prectingulum longer than in M^2 with V-shaped accommodation notch for M^2 metastyle.

M^4 (Fig. 3C). Tip of parastyle situated lingual to tip of M^3 metastyle; preparacrista slightly convex, about equal in length to M^3 ; metacone greatly reduced, Protoconule better developed than on other molars; metaconule absent; talon narrow; preprotocrista weak. A tiny styler cusp is situated midway between parastylar tip and base of metacone.

Meristic gradients, M^{1-4} (Fig. 3C). Preparacrista: increases posteriorly, M^{3-4} about equal; postmetacrista:

increases posteriorly except M^4 where absent; paracone height: increases posteriorly M^{1-3} , M^4 equals or slightly lower than M^3 ; metacone height: increases posteriorly, except M^4 where reduced; protocone height: decreases posteriorly; talon surface: increases posteriorly M^{1-2} , decreases posteriorly M^{3-4} ; stylar cusp B size: decreases M^{1-4} ; stylar cusp C: increases M^{1-3} , absent M^4 ; stylar cusp D: decreases M^{1-3} , absent M^4 ; stylar cusp E: decreases M^{1-2} , possibly M^3 , absent M^4 .

Dentary (Fig. 2C). Medial surface flat, digastric fossa faint, shallow; subalveolar fossa, lateral crest well-defined. Masseteric fossa deep with prominent shelf-like submasseteric crest. Depth of horizontal ramus below M_4 14.0 mm; thickness of inferior border at same level, 5.5 mm.

M_3 (Fig. 2C-F). Paraconid and protoconid bulky; metacristid nearly perpendicular to long axis of crown; talonid distinctly narrower than trigonid; metaconid large, higher than paraconid, bulky at base. Entoconid small but distinct; as high as hypoconulid; hypoconulid merges labially with postcingulid. Hypoconid lowest cusp on crown; pre- and postcingulids present but not strongly developed. Cusp heights: protoconid > metaconid > paraconid > entoconid = hypoconulid > hypoconid.

M_4 (Fig. 2C-F). Cusps of trigonid more slender, talonid greatly reduced compared to M_3 ; metaconid and paraconid similar in height to M_3 but more slender. Entoconid reduced to thickening of preentocristid, lower than hypoconulid; hypoconulid high pointed cusp, continuous labially with postcingulid. Pre- and postcingulids not strongly developed. Cusp heights: protoconid > metaconid > paraconid > hypoconulid > entoconid > hypoconid.

Meristic gradients M_{3-4} (Fig. 2C-F). protoconid, paraconid and metaconid decrease in bulk posteriorly; talonid decreases in width posteriorly; entoconid decreases in size posteriorly; angle of paracristid to long axis of crown more acute posteriorly.

Etymology. Named after Ian Archibald in honour of his contributions to the natural history of the Northern Territory.

Nimbacinus Muirhead and Archer, 1990

Type species. *Nimbacinus dicksoni* Muirhead and Archer, 1990, by original designation.

Niubacinus richi sp. nov.

(Fig. 5, Table 1)

Nimbacinus dicksoni - Muirhead and Archer 1990: fig. 3 (in part).

Diagnosis. Medium-sized thylacinid with narrow diastemata between premolars, P_3 much larger than P_2 ; lower molars with well-developed metaconids and entoconids. Differs from *Nimbacinus dicksoni* in possessing well-developed metaconids on M_{2-4} in

conjunction with reduced metaconid on M_1 and large conical entoconids on M_{1-3} ; differs from *Ngamalacinus timmulvaneyi* and *Badjcinus turnbulli* in lacking a carnassial notch in the hypocristid, and from *Wabulacinus ridei* Muirhead, 1997, and species of *Thylacinus* in having large metaconids.

Type material. HOLOTYPE - NTM P9612-4 (Top Site), right dentary with P_1 - M_4 ; canine, incisors missing. PARATYPE - NTM P85553-3 (unrecorded quarry), fragment of right dentary with P_{1-2} and M_1 (also a paratype of *N. dicksoni* Muirhead and Archer, 1990).

Type locality. 'Top Site', Bullock Creek, Northern Territory (additional data as for *Mutpuracinus archibaldi*).

Referred material. NTM P8695-92 (Blast Site), horizontal ramus of left dentary retaining P_2 , M_1 , M_{3-4} (M_3 lacking paraconid); P904-7 (Top Site), left dentary fragment retaining M_{2-4} .

Lithic unit, fauna and age. Camfield Beds, Bullock Creek Local Fauna, mid Miocene (additional information as for *Mutpuracinus archibaldi*).

Description. **Dentary** (Fig. 5A,B). P9612-4 is about 25% smaller than *Thylacinus macknessi* Muirhead, 1992, but relatively stouter anteriorly and more bowed along inferior border; anterior margin of ascending ramus more erect, condylar notch wider, more invasive. Diastema between P_2 - P_3 very short, approximately 1.4 mm; large mental foramen under posterior root of P_1 , small posterior mental foramen under posterior root of M_1 . Masseteric crest well developed, flange-like; masseteric fossa relatively shallower and condyle; condyle transversely elongate (14.0 mm wide), slightly flattened dorsally. Mandibular foramen situated 22.0 mm from distal edge of condyle; depth of ramus below M_4 is 15.6 mm; thickness of inferior border at same level is 7.0 mm.

Incisors, I_{1-3} (Fig. 5A,B). Three incisor alveoli present anteromedial to canine alveolus, arranged in a triangle, I_3 ventrolaterally, I_2 lingually and I_1 above I_2 but aligned vertically with I_3 ; I_3 socket smallest (1.3 mm x 1.5 mm) followed by I_2 (1.3 mm x 2.5 mm) with I_1 largest (1.5 mm x 3.0 mm); lateral width of all three sockets about 3 mm, vertical extent about 4.8 mm.

Canine (Fig. 5A,B). Alveolus only (7.4 mm vertical, 4.0 mm mediolateral) oval socket, anterolaterally directed.

Premolars, P_{1-3} (Fig. 5A,B). P_1 oriented obliquely (approximately 15°) to long axis of other premolars, much smaller than P_2 (5.0 mm long, 2.0 mm wide) with low, recurved protoconid and very elongated posterior shelf lacking distinct cuspule. Protoconid of P_2 much higher, longer than P_1 ; small anterobasal and posterobasal cuspules present (6.1 mm long, 2.8 mm wide); P_3 , anterobasal cuspule more defined, posterior shelf more talonid-like and elevated distally with small posterolingual and large posterobasal cuspules (7.2 mm long, 3.1 mm wide). Protoconids of all premolars directed posteriorly.

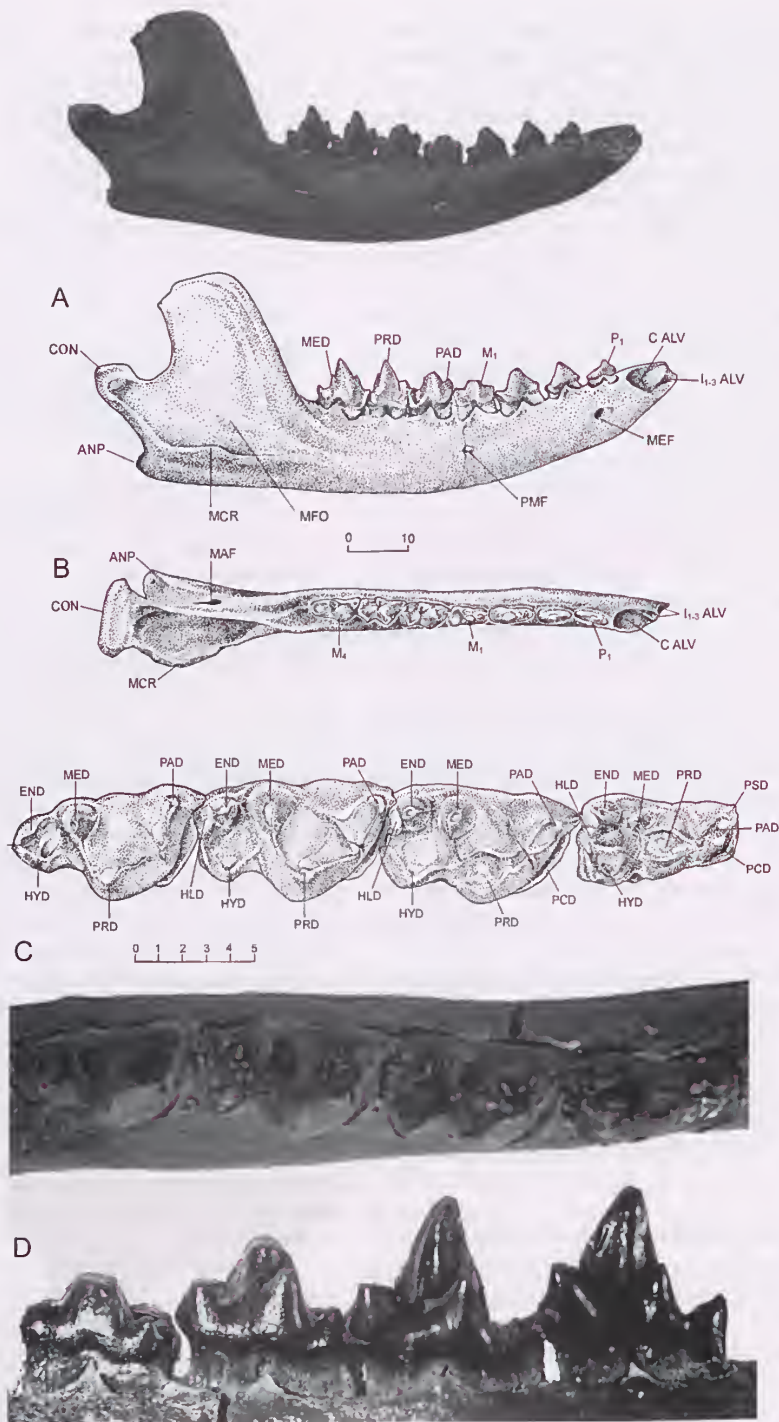


Fig. 5. *Nimbacinus richi* sp. nov. holotype right dentary (P9612-4) in: **A**, lateral view; **B**, occlusal view; **C**, molars M₁₋₄ in occlusal view; and **D**, molars M₁₋₄ in lateral view.

Molar, M_1 (Fig. 5A-D). Subrectangular crown, rather truncated anteriorly and markedly so posteriorly; talonid wider than trigonid; short paracristid slightly angled lingually, paraconid low, broad, conical with short preparacristid terminating in small parastylid; protoconid central, crown shallowly waisted on either side; posterolingual corner of talonid forming right angle; entoconid prominent, posteriorly-directed, conical cusp about 1.5 mm in diameter, separated from base of metaconid by deep, transverse groove; entoconid much larger and higher than hypoconulid; hypoconid large, triangular, lowest cusp on talonid. Small metaconid represented by low, broad triangular bulge on posterolingual side of protoconid. Pre- and postcingulids thick, well developed anterolabially, terminating above middle of anterior root; postcingulid ascends to just below hypoconulid. Cusp heights: protoconid > metaconid > entoconid > paraconid > hypoconulid = hypoconid.

M_2 (Fig. 5A-D). Trigonid somewhat compressed, much longer and slightly wider than talonid; paracristid slightly less obtuse than in M_1 ; metaconid much larger and more differentiated from protoconid; small carnassial notch present in metacristid; entoconid slightly larger and higher than in M_1 ; extending high above smaller, flat, triangular hypoconulid and closely adpressed to parastylid of M_3 . A short preentocristid developed. Hypoconulid extending distolabially a short distance beyond the entoconid where it is accommodated by distinct C-shaped notch between precingulid and parastylid. Hypoconid a broad, triangular cusp much lower than hypoconulid. Cristid obliqua ascending base of protoconid for short distance. Cusp heights: protoconid > metaconid > paraconid > entoconid > hypoconulid > hypoconid.

M_3 (Fig. 5A-D). Protoconid more slender than in M_2 , paraconid higher, slightly more erect, metaconid also higher, more differentiated, but more slender than in preceding molar; talonid shorter and narrower relative to trigonid than in M_2 . Entoconid reduced to small spur-like cusp on anterolingual margin of enlarged, triangular hypoconulid; hypoconulid projects distally into accommodation notch in M_4 . Postcingulid reaches labial side of hypoconulid; hypoconid situated much lower than in M_2 and considerably reduced; cristid obliqua ascends posterior face of protoconid about halfway up to carnassial notch. Cusp heights: protoconid > metaconid > paraconid > hypoconulid > entoconid > hypoconid.

M_4 (Fig. 5A-D). Paraconid directed slightly more to lingual side than in M_3 ; para- and metacristids blade-like, with deep carnassial notches; metaconid greatly reduced though fully differentiated from protoconid; talonid width about half that of preceding molar; entoconid reduced to thickening of the preentocristid; hypoconulid formed as in preceding molar, but smaller, succeeded anteriorly by strong posthypocristid;

postcingulid vestigial. Hypoconid small, situated low on posterolabial margin of talonid basin; talonid basin open labially; cristid obliqua strongly developed, ascends posterior face of protoconid to base of carnassial notch in metacristid. Cusp heights: protoconid > paraconid > metaconid > hypoconulid > entoconid > hypoconid.

Meristic gradients, M_{1-4} (Fig. 5A-D). Protoconid decreases in bulk posteriorly; paraconid increases in height and obliquity to long axis of crown posteriorly; metaconid increases markedly in bulk from M_1 to M_2 then gradually decreases; metaconid gradually increases in height to M_3 then decreases in M_4 ; entoconid increases in size and height to M_2 then decreases M_3 to M_4 ; hypoconulid increases in height posteriorly; hypoconulid increases in size posteriorly to M_3 then decreases in M_4 ; talonid increases in width from M_1 to M_2 then decreases from M_3 to M_4 .

Remarks. Association of referred specimens of lower molars with the uppers in *Nimbacinus dicksoni* was problematic (Muirhead and Archer 1990). Muirhead and Archer (1990) note several differences between the holotype M_1 (QMF16802, 'Henk's Hollow', Carl Creek Limestone) and the Bullock Creek Local Fauna specimen (P85553-3). The latter specimen shows a stronger entocristid and a more angular posterolingual corner, resulting in greater posterior crown width and a more rounded contour of the anterolingual surface. Although very worn, the entoconid of P85553-3 (difficult to see in their illustration) is somewhat larger and more distinct than that of the holotype. The same differences are more emphasised in less-worn P9612-4 in which a large, conical entoconid is present. These distinctions appear to be consistent and therefore not readily attributable to individual variation. More important however, is the status of paratype QMF16809 (Site D locality), identified as a right M_2 (their M_3 in Archer (1978, 1982) terminology). If this specimen, that has a greatly reduced metaconid, represents *N. dicksoni* (as they argue at some length), then P9612-4, which has a large metaconid on M_2 , could not represent this species. While a species-level distinction could be made on the basis of this technicality alone, the subsequent discovery of several similar-sized thylacinid species increases the probability that QMF16809 might not represent *N. dicksoni*, and therefore a systematic distinction made on this basis could be phylogenetically misleading. While the differences in M_1 morphology alone are sufficient to indicate the existence of another species of the genus *Nimbacinus*, this proposed revision leaves the states of the M_{2-4} metaconids of *N. dicksoni* in doubt.

Etymology. Named in honour of Thomas Rich for his many important contributions to vertebrate palaeontology in Australia. Tom introduced us to the Bullock Creek Local Fauna of the Northern Territory in 1984.

Tyarrpecinus gen. nov.

Type species. *Tyarrpecinus rothi* sp. nov. by monotypy.

Diagnosis. Medium-sized thylacinid with transversely narrow, elongate M^1 and strong ectoflex and elongation of metastylar spur on M^3 ; differs from *Muribacinus gadiyuli* and *Mutpuracinus archibaldi* in larger size, narrower M^1 , more elongate and slender metastylar wing; wider angle between preparacrista and postmetacrista; more closely approximated paracone and metacone on M^3 ; differs from *Badjcinus turnbulli* in form of premolar crown; in possessing stylar cusps and preparacrista on the anterior lobe of M^1 ; more reduced stylar cusp B and relatively larger stylar cusp D on M^3 ; differs from *Nimbacinus dicksoni* and *Ngamalacinus timmulvaneyi* in having a more slender, elongated M^1 with straighter centrocrista and more reduced parastylar spur; M^3 metastylar spur more elongate; narrower trigone basin, metacone larger relative to paracone; conules where present, extremely reduced; differs from *Wabulacinus ridei* in more transverse orientation of preparacrista and retention of stylar cusps B and D on M^1 ; differs from *Thylacinus macknessi* in reduction of precingulum but retention of stylar shelf, otherwise showing conservative *Thylacinus*-like apomorphies.

Etymology. Eastern Arrente dialect *tyarrpa* 'cracked' + *Kynos* (Gr.) 'dog'. *Tyarrpa*, pronounced char-puh, (Henderson and Dobson 1994), is in reference to the state of preservation of the type material.

Tyarrpecinus rothi sp. nov.

(Fig. 6, Table 1)

Diagnosis. As for genus.

Type material. HOLOTYPE - NTM P98211 (Main Pit), fragment of left maxilla with P^2 , M^1 - M^4 ; M^1 and M^3 complete but assembled from fragments; M^2 and M^4 represented by talons only; approximately 75 small fragments consisting of isolated roots and bone and enamel fragments.

Type locality. Alcoota Scientific Reserve, Northern Territory, Australia. 22°52' S, 134°52' E; Alcoota 1:250,000 Map Sheet, SF/53-10.

Lithic unit, fauna and age. Waite Formation, Alcoota Local Fauna, late Miocene on the basis of marsupial stage-of-evolution biochronology (Woodburne et al. 1985; Murray et al. 1993, Murray et al. 2000).

Description. The *Tyarrpecinus rothi* sp. nov. holotype, P98211, was reconstituted from a concentration of small fragments of bone and teeth that may represent the contents of a crocodilian coprolite. Many of the fragments show chemical erosion and are coated with a layer of calcite. Part of the left maxilla has been assembled and, except for some conspicuous cracks and a few missing chips of enamel, the M^1 and the M^3 have been adequately restored for description.

Maxilla. Maxilla contains P^2 and anterior alveolus of P^3 . A 4.5 mm long section of the diastema anterior to P^2 does not reach the P^1 alveolus. Palatal process extends to median palatal suture and is about 7.0 mm wide immediately anterior to P^2 . P^3 alveolus situated immediately posterior to P^2 and no diastema present. Anterior root socket of P^3 is about twice diameter of that of P^2 .

Premolar, P^2 . P^2 crown low and elongate basally. Cusp points posteriorly and anterior profile slightly convex. Posterior margin of crown distinctly concave. Surface of posterior shelf obscured by an obdurate calcite encrustation. Posterior root about twice as wide mesiodistally as anterior root. Crown length about 6.5 mm; width, 2.5 mm.

P^3 . Alveolus only; at least 7.3 mm total length (hypertrophied); anterior root socket about 3.0 mm long and 2.0 mm wide; posterior root socket at least 4.0 mm long, width unknown.

Molar, M^1 . Reconstructed from three fragments; heavily worn and thickly coated with calcite. Crown elongated, transversely narrow; short, distinct precingulum present; deep cleft divides crown into two lobes, shallow but distinct ectoflex. Stylar cusp B about same size as paracone; metacone about half again larger than paracone. Postmetacrista straight, angles slightly lingual to postprotocrista. Preparacrista short, extends transversely to long axis of crown to stylar cusp B. Centrocrista obtuse, essentially parallel to tooth row; stylar cusp D much smaller than metacone, closely situated distolabially and connected to it by low crest with conspicuous groove labial to metacone and mesial to stylar cusp D; small stylar cusp E heavily worn, but faintly visible. Talon short transversely with U-shaped profile. A very small metaconule represented. Cusp heights: metacone > stylar cusp B > stylar cusp D > paracone > protocone.

M^2 . Talon only, larger than M^1 talon and more V-shaped. Basin shallow, heavily worn on mesial side; conules absent; crest of base of metacone confluent with postprotocrista.

M^3 . Complete crown and roots, reconstructed from four fragments, moderate wear (slight misalignment of fragments due to missing slivers of dentine at contacts). Prectingulum short, complete; parastylar spur much shorter than metastylar spur, strong ectoflexus; stylar cusp B connected to paracone by convex, mesially-angled preparacrista; stylar cusp C reduced, but present; low elongated stylar cusp D produces conspicuous labial bulge; distinct, elliptical thickening of enamel in region of stylar cusp E, but no definite cusp structure visible. Metacone much larger and higher than paracone. Angle of centrocrista about 90°; angle between preparacrista and postmetacrista slightly wider than in *Nimbacinus dicksoni* and *Ngamalacinus timmulvaneyi*. Talon narrow,

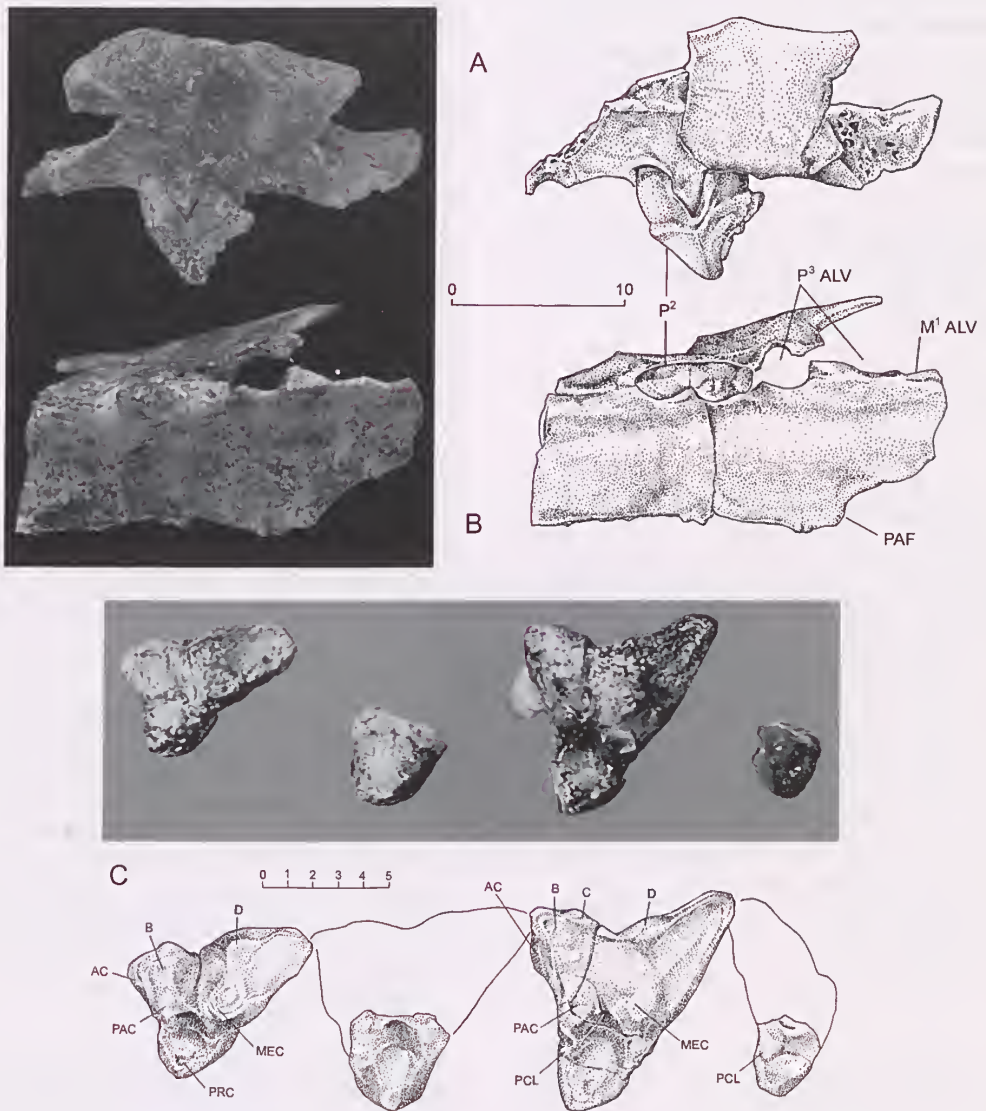


Fig. 6. *Tyarrpecinus rothi* gen. et sp. nov. holotype left maxilla (P98211). Maxillary fragment in A, lateral and B, occlusal views; C, reconstructed molar tooth row (M_{1-4} from left to right) in occlusal view. Scale bars in mm.

V-shaped, very faint protoconule evident, metaconule absent. Cusp heights: metacone > paracone > styler cusp D > ?styler cusp E = styler cusp B > styler cusp C > protoconule > protocone.

M^1 . Talon only; greatly reduced compared to M^3 ; narrow, V-shaped, with low protoconule.

Etymology. Named in honour of Karl Roth for his contributions to the natural history of Central Australia

and long career as Custodian of the Alice Springs branch of the Museums and Art Galleries of the Northern Territory, from which he recently retired.

PHYLOGENY RECONSTRUCTION

Muirhead and Wroc (1998) analysed shared, derived character states amongst five thylacinid genera to

reconstruct phylogeny in the family. Of 32 characters analysed, 24 are dental, with the remainder pertaining to the cranium. As a preliminary analysis, the states of the three newly described species plus *Muribacinus gadiyuli* Wroe, 1996, and *Thylacinus megiriani* Murray, 1997, were scored and added to their matrix (Table 2A - necessarily omitting the eight cranial characters) and analysed with Hennig86 version 1.5 (Farris 1988). One

Table 2. Thylacinid character expressions for phylogenetic analysis: A, following Muirhead and Wroe (1998), cranial characters 1, 2 and 4-9 omitted; B, preferred matrix as discussed in the text. Character definitions for matrices A and B given with Figures 7 and 8 respectively.

A													
Characters (Muirhead and Wroe 1998)	Dasyurid outgroup	<i>Muribacinus gadiyuli</i>	<i>Mutpuracinus archibaldi</i>	<i>Nimbacinus dicksoni</i>	<i>Nimbacinus richi</i>	<i>Badjacinus turnbulli</i>	<i>Ngamalacinus timmulvaneyi</i>	<i>Tjarrpecinus rothi</i>	<i>Wabulacinus ridei</i>	<i>Thylacinus macknessi</i>	<i>Thylacinus potens</i>	<i>Thylacinus megiriani</i>	<i>Thylacinus cynocephalus</i>
3	0	0	0	1	?	0	1	?	0	?	1	1	1
10	0	1	1	1	?	2	1	2	1	1	2	3	3
11	0	1	1	1	?	2	2	3	3	4	4	4	4
12	0	0	0	0	?	0	0	1	1	0	1	2	2
13	0	0	0	0	?	2	1	2	1	2	2	3	3
14	0	0	0	0	?	1	1	2	2	2	2	2	2
15	0	1	1	1	?	1	1	2	2	2	2	2	2
16	0	0	0	0	?	3	0	1	2	1	1	1	1
17	0	1	1	1	?	1	1	2	2	2	2	2	2
18	0	0	0	0	1	1	0	?	0	0	0	0	0
19	0	1	1	1	1	1	2	?	3	4	4	?	4
20	0	1	1	2	0	1	0	?	4	3	3	?	3
21	0	0	0	0	0	0	1	?	0	0	0	?	0
22	0	0	?	0	0	0	0	?	1	0	0	?	0
23	0	0	?	0	1	0	?	?	?	1	1	?	1
24	0	1	1	1	1	1	2	?	3	4	5	?	5
25	0	0	0	0	1	1	1	?	0	0	0	?	0
26	0	0	0	0	0	0	1	?	0	1	1	?	1
27	0	1	1	1	2	1	2	?	1	3	3	?	3
28	0	0	0	0	0	1	1	?	0	0	0	?	0
29	0	1	1	1	2	1	2	?	2	3	3	?	3
30	0	0	?	1	1	0	?	?	1	1	1	?	1
31	0	?	0	0	0	0	1	?	1	1	1	?	1
B													
Characters (this work)													
1	0	0	1	2	2	2	2	?	3	3	4	?	4
2	0	0	0	0	0	1	1	0	0	0	0	0	0
3	0	0	0	0	0	0	0	1	1	1	1	1	1
4	0	0	0	0	0	0	0	0	1	1	0	0	0
5	0	0	0	0	0	0	0	1	0	0	1	1	1
6	0	0	0	0	0	0	0	0	1	1	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	1	1
8	0	0	0	0	0	0	0	1	1	1	1	1	1

of eight equally parsimonious hypotheses selected for discussion purposes is shown as Figure 7A, and the Nelsen consensus tree is shown as Figure 7B.

In Figures 7A and 7B, the previously analysed species branch consecutively in the same order as illustrated in Muirhead and Wroe (1998). Of the new species, *Mutpuracinus archibaldi* aligns with the plesiomorphic *Muribacinus gadiyuli* at the base, and *Tjarrpecinus rothi* branches off after *Ngamalacinus ridei* and *Wabulacinus*.

The emphasis in Muirhead and Wroe (1998) on ordered multistate characters, postulating broad morphoclines for the majority of character states, tends to relegate resulting trees to a hierarchy of structural grades. Notwithstanding, there are some promising synapomorphic states that suggest clade formation within the consecutively branched dendrogram. These include the synapomorphic occurrence of a carnassial notch in the hypocristid of *Badjacinus* and *Ngamalacinus* (Character 28 in Table 2A) and mutual loss of stylar cusp B accompanied by extreme reduction of the stylar shelf in *Wabulacinus ridei* and *Thylacinus macknessi* (Character 11); which, in combination with the strongly morphoclineal expression of metaconid reduction (Characters 18-19) result in the more resolved hypotheses (Fig. 8 based on the character matrix in Table 2B) preferred here.

Muirhead and Wroe (1998) divide the character of metaconid reduction into two sets, Character 18, in which a differential absence of metaconid on M₁ and presence on the other molars is scored autapomorphically among thylacinids for *Badjacinus*, and Character 19 in which the size of metaconids on M₂₋₄ is scored as an independent multistate set. The recognition of a unique differential reduction of the metaconid in *Badjacinus* is apparently based on the assumption of uniformly reducing metaconids in *Nimbacinus dicksoni*, as indicated by the D-Site M₂ paratype, QMF16809.

However, *Nimbacinus richi* shows a similar degree of differential metaconid expression to that of *Badjacinus*, in which the cusp is nearly obsolete on M₁, but well-differentiated and large on M_{2,3}, then reduced on M₄. Thus, while the extent of metaconid reduction on M₁ in *Badjacinus* is more advanced than in *Nimbacinus richi*, we do not consider the character of differential expression of the metaconid to be unique to *Badjacinus* (within the Thylacinidae). The states of metaconids in *N. richi* also negate the proposition that the expression gradient of the metaconid along the molar row is typically uniform in thylacinids. In any case, the differential reduction of metaconids in *Badjacinus turnbulli*, *Nimbacinus richi* and *Ngamalacinus timmulvaneyi* may be the rule rather than the exception, and as such, the basic similarity of the differentially reduced states of the metaconids in these species is probably more meaningful for thylacinid phylogeny than the autapomorphic absence of a metaconid on M¹ in *Badjacinus*.

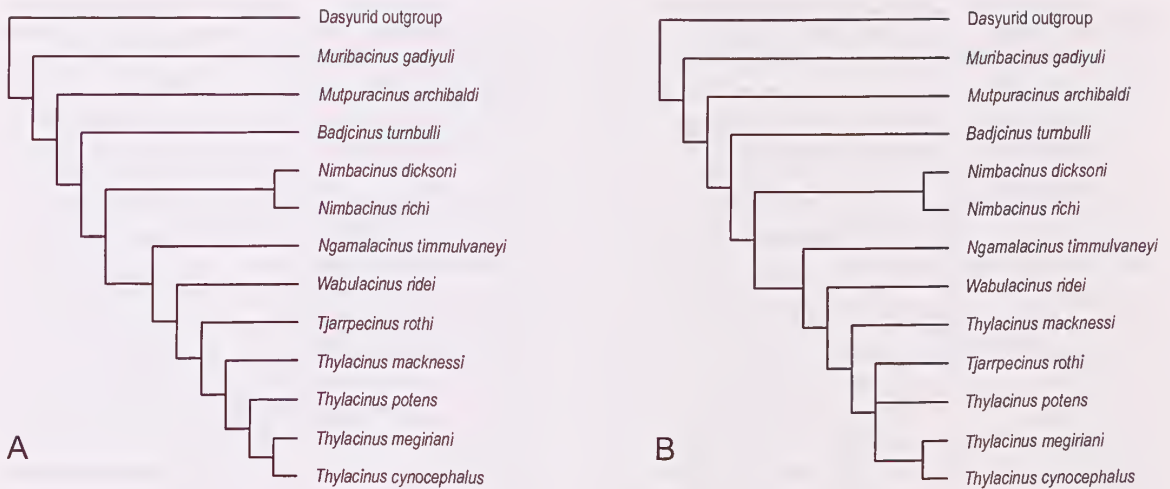


Fig. 7. A, one of eight equally parsimonious trees depicting thylacinid phylogeny using character matrix after Muirhead and Wroe (1998) (see Table 2A of this work); B, Nelsen consensus of the eight equally parsimonious trees (Consistency Index = 0.73; Retention Index = 0.85; Hennig86 version 1.5 (Farris 1988)). *Abridged definitions of character expressions* (see Muirhead and Wroe 1998 for details). 3, infraorbital foramen: 0, not bounded by jugal; 1 bounded by jugal. 10, size of paracone: 0, equivocal plesiomorphic state; 1, slight reduction; 2, significant reduction; 3, extreme reduction. 11, styler cusp B: 0, well developed; 1, slight reduction; 2, greater reduction; 3, more reduced yet; dramatically reduced [Muirhead and Wroe (1998) include the styler shelf and styler cusp D in this morphocline; actual loss or extreme reduction of styler cusp B in thylacinids is confined to *Thylacinus macknessi* and *Wabulacinus ridei* (Muirhead 1992, 1997).] 12, anterior cingulum: 0, complete; 1, incomplete. 13, protocone and conules: 0, well developed; 1, slightly reduced; 2, significant reduction; 3, conules lost. 14, length postmetacrista: 0, as in dasyurids; 1, slight elongation. 15, angle centrocrista: 0, acute; 1, more obtuse than in dasyurids; 2, colinear. 16, direction of preparamacrista: 0, perpendicular; 1, slightly oblique; 2, parallel to long axis; 3, directly anterior to paracone. 17, angles preparamacrista and postmetacrista: 0, narrow; 1, slightly widening; 2, wider yet. 18, size of metaconid in M_1 relative to M_{2+4} : 0, uniform reduction; 1, variably absent on M_1 , present M_{2+4} ; 19, size metaconid M_{2+4} : 0, plesiomorphic condition; 1, some reduction; 2 more reduced; nearly lost; 4, lost. 20, size entoconid: 0, large; 1, slight reduction; 2, greater reduction; 3, very reduced; 4, absent. 21, morphology entoconid: 0, plesiomorphic condition; 1, laterally compressed. 22, diastema P1-2: 0, present; 1, absent. 23, diastema P2-3: 0, present; 1, absent. 24, hypoconulid / hypoconulid notch: 0, present; 1, slightly diminished; 2, obvious reduction; 3, more reduced yet; 4, extremely reduced; 5, notch absent. 25, posterior cingulid and hypocristid: 0, separated; 1, joined. 26, cristid obliqua carnassial notch: 0, absent; 1, present. 27, angle hypocristid: 0, parallel to transverse axis of dentary; 1, moderate angle; 2, intermediate; 3, pronounced. 28, carnassial notch in hypocristid: 0, absent; 1, present. 29, termination of cristid obliqua: 0, low; 1, higher; 2, stronger, higher; 3, principle posterior shearing crest. 30-31, size P3, two pathways: 00, 01, plesiomorphic; 10 apomorphic [see Muirhead and Wroe (1998) for explanation.] 32, length M_4 : 0, shorter than M_3 ; longer than M_3 .

The inclusion of *Muribacinus gadiyuli* and *Mutpuracinus archibaldi* present a fairly complete picture of the morphocline for metaconid reduction in thylacinids: *Muribacinus gadiyuli* shows gradual posterior enlargement of the metaconids (0); *Mutpuracinus archibaldi* shows a slight reduction in the size of M_4 metaconid (1), (M_{1+2} unknown); *Ngamalacinus timmulvaneyi* shows marked reduction of metaconid on M_1 and M_4 ; *Nimbacinus richi* shows further reduction of metaconid on M_1 with no further reduction on M_4 than in the former species, and *Badjcinus turnbulli* shows complete loss of metaconid on M_1 with no further reduction on M_4 than in the former species (2); while the metaconid is nearly obsolete on all molars of *Wabulacinus ridei* and *Thylacinus macknessi* (3) and lost on all other species of *Thylacinus* (4).

Resolution of clade formation is obscured by the establishment of several interrelated morphoclines

(widened angle of preparamacrista and postmetacrista, straightened centrocrista, elongation of postmetacrista, styler shelf and cusp reduction) expressing progressive states of carnassialisation in the Thylacinidae. These overwhelm the otherwise compelling evidence for at least two parallel trends in development of longer shearing crests while simultaneously suppressing the relatively few synapomorphic states that might otherwise have been recognised by the algorithm. While it is true that there is a general trend towards increased carnassialization signalled among these genera, and that the structural changes that characterise these trends are essentially indistinguishable (the possible exception being *T. macknessi* - Muirhead 1992: 72), the disjunct nature of the character combinations indicate that the similarities in the states of carnassialization between *Thylacinus macknessi*, *Wabulacinus ridei* and the comp-

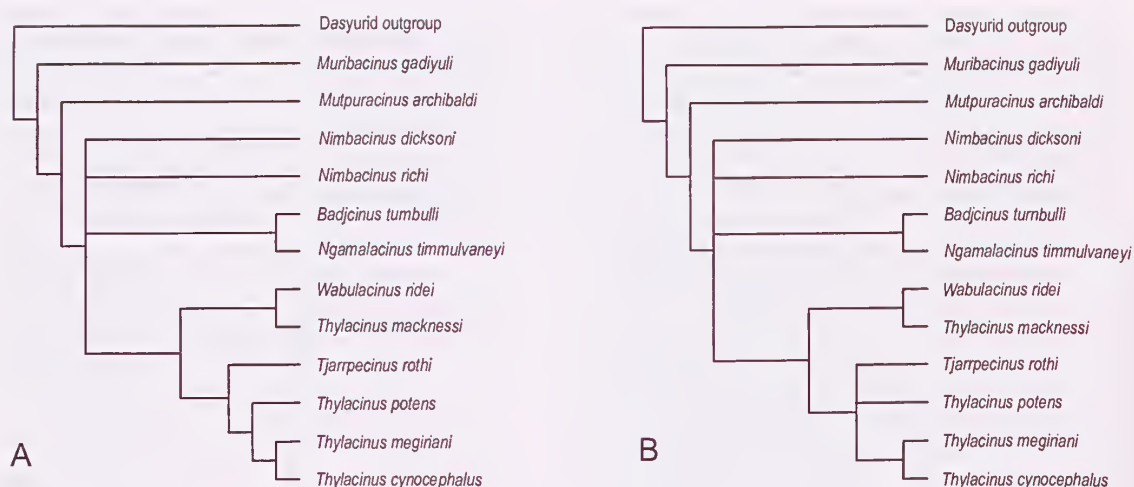


Fig. 8. Dendrograms (A, more, and B, less, resolved) depicting preferred hypotheses of thylacinid phylogeny based on a restricted suite of characters (Table 2B) which do not include the autapomorphic and discontinuous characters of Table 2A. (Hennig86 version 1.5 (Farris 1988); 2 equally parsimonious trees; Consistency Index = 1.0; Retention Index = 1.0). *Definitions of character expression.* 1, pattern of metaconid reduction: 0, slight, uniform; 1, slight M_2 ; 2, differential, marked on M_1 , slight M_2 ; 3, near obsolescence on all molars; 4, entirely lost on all molars. 2, carnassial notch in hypocristid: 0, absent; 1, present. 3, elongation of postvallum, shearing surfaces: 0, slight; 1, significant. 4, stylocone B: 0, present; 1, extremely reduced or lost. 5, paracone reduction / hypertrophy of metacone: 0, slight – moderate; 1, conspicuous. 6, ectoflexus: 0, strong expression; 1, weak expression. 7, precingulum: 0, present, strong; 1, reduced – absent. 8, entoconid: 0, distinct; 1, reduced – absent.

ably derived species of *Thylacinus* are phylogenetically uninformative homoplasy.

As Muirhead (1992, 1997) and Muirhead and Gillespie (1995) point out, both *Wabulacinus ridei* and *Thylacinus macknessi* show progressive states of carnassialization (loss of styler cusps, extreme reduction-loss of styler shelf, lengthening, straightening of crests) in combination with several autapomorphies and retained plesiomorphies (relatively unreduced paracones). Whereas in *Tyarrpecinus* and other members of *Thylacinus*, carnassialization has proceeded in conjunction with plesiomorphic retention of the styler shelf, styler cusps and apomorphic reduction of paracone and/or enlargement of metacone. In other words, the crown genera share an ancestor with states close to *Nimbacinus*, rather than, as the Muirhead and Wroe (1998) cladogram implies, direct, successive sister relationships with *Wabulacinus ridei* and *Thylacinus macknessi*.

Tyarrpecinus rothi is therefore considered to represent the plesiomorphic sister-taxon of the *Thylacinus* clade (*T. potens* + *T. meginiani* + *T. cynocephalus*, but not *T. macknessi*) (Fig. 8A,B), as it is too derived (more reduced M^1 paracone and precingulum) to have given rise to *Thylacinus macknessi* and probably *Wabulacinus ridei* (greater paracone reduction on M^1) while lacking highly derived states of styler cusp and styler shelf reduction/loss of the *Thylacinus* clade. *Tyarrpecinus rothi* shows incipient to moderate

development of *Thylacinus*-like states in the considerable reduction of the parastylar spur, reduction of the precingulum, elongation of the postmetacrista; mesial obliquity of the preparacrista, reduction of the paracone, extreme reduction to loss of conules and reduction of the trigone basin on M^3 . Resemblance to particular species of *Thylacinus* are evident, such as strong ectoflex present in *T. potens* and *T. meginiani* M^3 . There is also the question of the expression of a tiny styler cusp E which appears to be present in the form of an elliptical thickening of the styler crest of M^3 in both *Tyarrpecinus* and *Thylacinus meginiani* (Murray 1997). Although Muirhead and Wroe (1998) have concluded that the tiny styler cusp on the M^3 of *Thylacinus cynocephalus* represents a distally-shifted styler cusp D, we prefer to wait for additional data.

Other than some minor shifts in emphasis on some of the character states, the new data present no significant points of disagreement with recently proposed hypotheses of thylacinid phylogeny (Muirhead and Archer 1990, Muirhead 1992, Muirhead and Gillespie 1995, Wroe 1996, Murray 1997, Muirhead and Wroe 1998). However, the problem of association of the upper and lower molars of *Nimbacinus dicksoni* creates an ambiguity in character states of a pivotal group. The D-Site M_2 (QMF16809) has a much narrower paraconid and much smaller metaconid than the equivalent molar of the Bullock Creek LF *Nimbacinus* (P9612-4), so we are certain that it represents a different taxon, probably

another genus, in concert with the current level of systematic discrimination. However, the Bullock Creek LF specimens (P85553-3 and P9612-4) are sufficiently close to the holotype M₂ (QMF16802) to indicate a species-level distinction, and accordingly, we have inferred that the unknown M_{2,3} of *N. dicksoni* are as similar to *N. richi* as is the M₁.

Although poorly represented, the *Tyarrpecinus rothi* morphotype is sufficiently generalised to represent the structural stage that may have given rise to all *Thylacinus* species except *T. macknessi*, and perhaps to *Wabulacinus ridei*. On the basis of present information, *Thylacinus macknessi* branched off from a less derived form than *Tyarrpecinus*. Taking the few synapomorphies between *Wabulacinus* and *Thylacinus macknessi* at face value, they become, more or less by default, sister taxa in a minor clade (Fig. 8A,B) characterised by progressive, predominantly homoplasious carnassialization. Muirhead and Archer's (1990) observations on some strong similarities between *N. dicksoni* and *T. potens* Woodburne, 1967, become more pertinent here, because, as they suggest, the well-developed ectoflexus in *N. dicksoni* may constitute a synapomorphic condition. With the additions of *Mutpuracinus archibaldi*, *Tyarrpecinus rothi* and *Thylacinus megiriani*, all of which display strong ectoflexus on M³, we are inclined to favour the interpretation of a symplesiomorphy retained in a conservative lineage culminating with the genus *Thylacinus*.

STRATIGRAPHIC PALAEONTOLOGY AND BIOCHRONOLOGY

The newly described Bullock Creek and Alcoota LF species brings the total number of ?late Oligocene and

Miocene thylacinids to 11 species in eight genera, all but *Nimbacinus* and *Thylacinus* being monospecific. No species are represented by abundant material, and thylacinids are presently of minimal use in intraformational biocorrelation and of no use in intracontinental correlation (Table 3). Even at the generic level, a high degree of faunal regionalism is indicated, which follows the general pattern observed by Rich (1991) for the Australian mid Tertiary vertebrate record.

There is stratigraphic evidence of sympatry for: *Mutpuracinus archibaldi* + *Nimbacinus richi* ('Top Site', Camfield Beds); *Ngamalacinus timmulvaneyi* + *Wabulacinus ridei* ('Camel Sputum Site', Carl Creek Limestone); *Thylacinus macknessi* + *Muribacinus gadiyuli* ('Gag Site', Carl Creek Limestone) and *Thylacinus potens* + *Tyarrpecinus rothi* (Waite Formation - two excavation sites, 'Main Pit' and 'Paine Quarry', sampling the Alcoota LF horizon) (Table 4). Although the 'Top Site' (Camfield Beds) assemblage is drawn from several lithofacies (Murray and Megirian 1992), and therefore possibly different beds, P9215-4 (*Nimbacinus richi*) and P9215-5 (*Mutpuracinus archibaldi*) were found lying one upon the other in the same block of limestone.

The only biostratigraphic evidence of temporal succession amongst thylacinids comes from superposition in the Waite Formation of *Thylacinus megiriani* (Ongeva LF) over *Thylacinus potens* and *Tyarrpecinus rothi* (Alcoota LF) (Murray *et al.* 1993; Megirian *et al.* 1996; Murray 1997; Megirian 2000), but a broader interpretive perspective is provided by zygomaturine stage-of-evolution biochronology (Woodburne *et al.* 1985; Megirian 1994; Murray *et al.* 2000) (Table 5). The as yet un-named species of *Neohelos* from the Camfield Beds and Carl Creek Limestone 'Gag' and 'Henks

Table 3. Stratigraphic distribution of ?late Oligocene and Miocene species of Thylacinidae, and biocorrelation of fossil assemblages.

Formation (geographic location)	Local Fauna	Site / Quarry	Species
Waite Formation (Alcoota)	Ongeva	South Quarry	<i>Thylacinus megiriani</i>
	Alcoota	Paine Quarry	<i>Thylacinus potens</i>
	Alcoota	Main Pit	<i>Tyarrpecinus rothi</i>
Camfield Beds (Bullock Creek)	Bullock Creek	Top Site	<i>Mutpuracinus archibaldi</i>
	Bullock Creek	Top Site	<i>Nimbacinus richi</i>
	Bullock Creek	Blast Site	<i>Nimbacinus richi</i>
Carl Creek Limestone (Riversleigh)		Camel Sputum	<i>Ngamalacinus timmulvaneyi</i>
		Inabeyance	<i>Ngamalacinus timmulvaneyi</i>
		Camel Sputum	<i>Wabulacinus ridei</i>
		D-Site	<i>Nimbacinus dicksoni</i>
		Henks Hollow	<i>Nimbacinus dicksoni</i>
		Gag	<i>Muribacinus gadiyuli</i>
		Gag	<i>Thylacinus macknessi</i>
		Nevilles Garden	<i>Thylacinus macknessi</i>
		Mikes Menagerie	<i>Thylacinus macknessi</i>
		White Hunter	<i>Badjcinus turnbulli</i>

Table 4. Stratigraphic evidence of sympatry amongst Miocene thylacinids.

Formation	Local Fauna	Site	Species
Waite Formation	Ongeva	South Quarry	<i>Thylacinus negiriani</i>
	Alcoota	Paine Quarry	<i>Thylacinus potens</i>
		Main Pit	<i>Tyarrpecinus rothi</i>
Camfield Beds	Bullock Creek	Top Site	<i>Mutpuracinus archibaldi</i>
		Top Site	<i>Nimbacinus richi</i>
		Blast Site	<i>Nimbacinus richi</i>
Carl Creek Limestone		Camel Sputum	<i>Ngamalacinus timmulvaneyi</i>
		Camel Sputum	<i>Wabulacinus ridei</i>
		White Hunter	<i>Badjacinus umbulli</i>
		Gag	<i>Muribacinus gadiyuli</i>
		Gag	<i>Thylacinus macknessi</i>
		Inabeyance	<i>Ngamalacinus timmulvaneyi</i>
		Henks Hollow	<i>Nimbacinus dicksoni</i>
		D-Site	<i>Nimbacinus dicksoni</i>
		Mikes Menagerie	<i>Thylacinus macknessi</i>
		Nevilles Garden	<i>Thylacinus macknessi</i>

Hollow' sites (Murray *et al.* 2000) is here identified as '*Neohelos* sp. nov.'. The following conclusions can be drawn from Table 5.

1. The apparent contemporaneity of *Nimbacinus richi* (Camfield Beds) and *Nimbacinus dicksoni* (Carl Creek Limestone) in *Neohelos* sp. nov. time suggests that these were allopatric sibling species.

2. *Thylacinus macknessi* lived at Riversleigh from *Neohelos tirarensis* to *Neohelos* sp. nov. time, which Murray *et al.* (2000) suggest may have spanned the latest Oligocene to mid Miocene. If 'D-Site' *Nimbacinus dicksoni* is actually conspecific with 'Henks Hollow' *N. dicksoni* as proposed by Muirhead and Archer (1990), then this taxon may have had a similar temporal range. Alternatively, the 'D-Site' *Nimbacinus* material may represent a different species, as discussed in the Systematics section above, which could conceivably represent the ancestor of one or both of *Nimbacinus dicksoni* and *N. richi*.

3. Five species of thylacinid may have co-existed at Riversleigh during *N. tirarensis* time, supporting the conclusions of Muirhead (1997), Muirhead and Wroe (1998) and of this study that a major phylogenetic radiation of thylacinids occurred before the ?late Oligocene (= pre *N. tirarensis* time).

4. No potential ancestor-descendent relationships have been identified amongst the 11 known Miocene thylacinid species: *Mutpuracinus archibaldi* is identified above as having structural states that may reflect the ancestral conditions giving rise to *Nimbacinus dicksoni*, but a phyletic succession from *M. archibaldi* to *N. dicksoni* is not consistent with biochronological indications in that *Mutpuracinus archibaldi* post-dates the earliest record of *Nimbacinus dicksoni*.

Estimating changes in thylacinid diversity through the Miocene is problematic due to different taphonomic processes at the very few known fossil-producing localities. Remains of small taxa are rare in the ephemeral channel and overbank deposits of the Waite Formation, and small terrestrial animals are sparse in the billabong and channel deposits of the Camfield Beds (Murray and Megirian 1992). Persistent sampling over many years produced the three new species reported here. In contrast, the small-scale cave-entrance/perched springline, fluvial tufa and associated pond deposits of the *N. tirarensis* biochron of the Carl Creek Limestone are noted for their preservation of small and medium-sized animals (e.g. Archer *et al.* 1989, 1991; Megirian 1992, 1997). The apparent decline in diversity in the Carl Creek Limestone from five species during *Neohelos tirarensis* time to two species during *Neohelos* sp. nov. time, with no species reported yet from apparently younger zygomatic biochrons, may also reflect preservational and sampling biases.

The association of quite highly advanced and very conservative forms in the Carl Creek Limestone during *N. tirarensis* time (e.g. *Thylacinus macknessi* + *Muribacinus gadiyuli*) reflects the extent of independent (parallel) evolution of lineages which emerged in the Palaeogene, including the crown group comprising the Waite Formation species and culminating in the recently extinct 'Tasmanian wolf', *T. cynocephalus*. It appears, from absence in the later fossil record, that by the late Miocene (*Kolopsis torus* time), all the conservative lineages as well as the quite advanced *Thylacinus macknessi* + *Wabulacinus ridei* clade, had become extinct, but the pattern of succession is not clear.

Table 5. A, thylacinid biochronology in terms of zygomaturine stage-of-evolution (Murray et al. 2000): *Neohelos tirarensis* stage ≡ latest Oligocene / early Miocene; *Neohelos* sp. nov. stage ≡ middle Miocene; *Kolopsis torus* stage ≡ late Miocene; *K. yperus* stage ≡ latest Miocene. * No *Neohelos* has been described from Carl Creek Limestone White Hunter Site, which is here tied in by simple marsupial biocorrelation, **B**, using burramyids (Brammall and Archer 1997), macropodids (Cooke 1997: table 1), phascolarctids (Black and Archer 1997) and the diprotodontoid *Bematherium angulum* (Black 1997: fig.1). White Hunter clusters with sites containing *N. tirarensis*, using Bray and Curtis agglomeration analysis and flexible UPGMA (Un-weighted Pair Group Method, Arithmetic average) algorithms in PATN (Belbin 1994).

A

Formation	Local Fauna	Site	Thylacinid species	Zygomaturine stage-of-evolution (Murray <i>et al.</i> 2000)
Waite Formation	Ongeva	South Quarry	<i>Thylacinus megiriani</i>	<i>Kolopsis yperus</i> (+ <i>Kolopsis torus</i>)
-unconformity-				
Waite Formation	Alcoota	Paine Quarry	<i>Thylacinus potens</i>	<i>Kolopsis torus</i>
Waite Formation	Alcoota	Main Pit	<i>Tyarrpecinus rothi</i>	<i>Kolopsis torus</i>
Camfield Beds	Bullock Creek	Top	<i>Mupuracinus archibaldi</i>	<i>Neohelos</i> sp. nov.
Camfield Beds	Bullock Creek	Top	<i>Nimbacinus richi</i>	<i>Neohelos</i> sp. nov.
Camfield Beds	Bullock Creek	Blast	<i>Nimbacinus richi</i>	<i>Neohelos</i> sp. nov.
Carl Creek Limestone		Gag	<i>Muribacinus gadiyuli</i>	<i>Neohelos</i> sp. nov.
Carl Creek Limestone		Gag	<i>Thylacinus macknessi</i>	<i>Neohelos</i> sp. nov.
Carl Creek Limestone		Henks Hollow	<i>Nimbacinus dicksoni</i>	<i>Neohelos</i> sp. nov.
Carl Creek Limestone		Camel Sputum	<i>Ngamalacinus timmulvaneyi</i>	<i>Neohelos tirarensis</i>
Carl Creek Limestone		Camel Sputum	<i>Wabulacinus ridei</i>	<i>Neohelos tirarensis</i>
Carl Creek Limestone		Inabeyance	<i>Ngamalacinus timmulvaneyi</i>	<i>Neohelos tirarensis</i>
Carl Creek Limestone		D-Site	<i>Nimbacinus dicksoni</i>	<i>Neohelos tirarensis</i>
Carl Creek Limestone		Mikes Menagerie	<i>Thylacinus macknessi</i>	<i>Neohelos tirarensis</i>
Carl Creek Limestone		Nevilles Garden	<i>Thylacinus macknessi</i>	<i>Neohelos tirarensis</i>
Carl Creek Limestone		White Hunter	<i>Badjcinus turnbulli</i>	(<i>Neohelos tirarensis</i>)*

B

Site	<i>Burramys brutyi</i>	<i>Bulungamaya delicata</i>	<i>Wabularoo uaughtoni</i>	<i>Ganawamaya sp2</i>	<i>Balbaroo gregoriensis</i>	<i>Nambaroo sp5</i>	<i>Nowidgee matrix</i>	<i>Litokoola kanunkaensis</i>	<i>Nimiookoola greystauesi</i>	<i>Bematherium angulum</i>	<i>Neohelos sp. nov.</i>	<i>Neohelos tirarensis</i>
Gag	1	1		1				1			1	
Henks Hollow	1			1				1			1	
Mikes Menagerie			1									1
Camel Sputum	1	1	1		1	1	1		1			1
Nevilles Garden	1	1	1		1	1			1			1
Inabeyance	1				1				1			1
D-Site		1	1							1		1
White Hunter	1		1				1			1		*

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Records of cetacean strandings in the Northern Territory of Australia

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ABSTRACT

Fifty-seven cetacean strandings are here documented for the Northern Territory (NT) coastline. This total includes events discovered in the course of Parks and Wildlife surveys, chance encounters reported by a variety of observers, and records held by various other government agencies and institutions. A total of 35 of these records are identified to species, seven to genus (*Globicephala*, *Balaenoptera*), and the remainder can be listed only as 'dolphin' (3), 'beaked whale' (1) or 'not known' (11). Of 26 species known to occur in Australia's tropical waters only 12 had previously been confirmed for the NT, and two others were provisionally listed on the basis of specimen material requiring further analysis. Strandings reported here include 10 of those 12 species and verify the two previously listed as uncertain (*Globicephala macrorhynchus*, *Kogia sinus*). The total confirmed list for NT waters (within three nautical miles of the coast) is further expanded to 16 species, now including the melon-headed whale *Peponocephala electra* (2 strandings) and killer whale *Orcinus orca* (sighting). A further species, the sei whale *Balaenoptera borealis* (trawled carcass), can also be added to the Commonwealth waters (within two hundred nautical miles) off the NT coast.

KEYWORDS. cetaceans, whales, dolphins, strandings, Northern Territory, Australia.

INTRODUCTION

With the inclusion of offshore islands and estuary systems, the Northern Territory coastline is over 10,000 km in length. For the most part it is of low relief, consisting mainly of sand beaches and mangrove flats, interrupted by headlands which seldom rise above 30 m. Because much of this coast is remote and sparsely inhabited, discoveries of stranded cetaceans are highly fortuitous events, and often their remains are quickly lost or scattered because under tropical conditions, carcasses rapidly disintegrate. Aborigines do encounter beached cetaceans from time to time, but difficulties of communication and traditional concerns mean that few of these incidents are likely to be reported.

A potentially important source of sightings are Coastwatch flights, which are conducted along the entire Northern Territory coast on a fairly frequent basis, but the primary objective is surveillance of human activities. Recently stranded single large whales, small groups and schools are detected from time to time, and are reported, but decomposing and partly buried carcasses are likely to be passed unnoticed.

Over the past ten years one of us (RC) has conducted numerous surveys of terrestrial wildlife in coastal areas on the ground and from the air. Incidental encounters with stranded cetaceans were investigated as a matter of routine, but were usually limited by the means then in hand and unfortunately the salvage of specimen material

was generally impractical. This paper summarises these direct observations on beached cetaceans or their remains, as well as reliable reports received by wildlife authorities from other observers, and documented records held both by the Museum and Art Galleries of the Northern Territory (MAGNT), Darwin, and by the National Cetacean Stranding Database (NCSD) maintained by Environment Australia, Canberra. Such a summary of cetacean strandings in the Northern Territory has not been attempted in the past.

METHODS

Information on strandings from all sources other than newspapers, which have not been searched, has been collated according to the following format: Species, Date, Locality (including latitude/longitude) and Comments. The primary date given is qualified by the term 'stranded' (which is either the known date of stranding or an estimated recent date if the specimen(s) was found dead in fresh condition), or the term 'found' in cases where specimens were decomposing or skeletal; otherwise it is simply the date a report was received. Doubtful circumstances are explained under Comments. Locality is given as a latitude and longitude and then described with reference to named topographical features, although in some instances this and the coordinates can only be approximations. The systematic order of the records listed in this paper follows Bannister *et al.* (1996).

Specimens retained by MAGNT and referred to in this paper are listed using a reference number commencing with 'U'. Records taken from the NCSD and used in this paper are listed by NCSD followed by their number on that database.

Other abbreviations used in this paper include: NT (Northern Territory), PWCNT (Parks and Wildlife Commission of the Northern Territory), DPIF (Department of Primary Industries and Fisheries) and *NT News* (Northern Territory News).

SYSTEMATIC LIST OF CETACEANS STRANDED IN THE NORTHERN TERRITORY

Family Delphinidae

Sousa chinensis - Indo-Pacific hump-backed dolphin

Date. Found August 1948.

Locality. 12°15'S, 136°54'E. Yirrkala, near Gove.

Comments. Johnson (1964) reports four mandibles, likely of three different animals, that were picked up off the beach by Aboriginal children during the American-Australian scientific expedition to Arnhem Land. Measurements and teeth counts are given in Johnson (1964).

Date. Stranded 23 November 1985.

Locality. 12°21'S, 130°52'E. Casuarina Beach, Darwin.

Comments. Single carcass washed ashore in fresh condition, male, length 2.08 m. Skull, mandibles and teeth collected by B. Freeland, PWCNT. Condylbasal length 510 mm, width 185 mm and height 175 mm; 30 teeth alveoli in one maxillary row and 32 teeth alveoli in one mandible. Photographs in PWCNT file P1999/629. Skull and mandibles in MAGNT, registered # U254. NCSD # 180.

Date. Found 28 October 1988.

Locality. 13°10'S, 130°07'E. Channel Point, opposite North Peron Island

Comments. Skull, lacking mandibles, condylbasal length 505 mm, width 220 mm and height 190 mm; 30 tooth alveoli in maxillary row. Collected by D. Neal. No further details. Skull in MAGNT, registered # U528.

Date. Stranded c. 2 March 1996.

Locality. 11°20'S, 132°07'E. Klocker Bay, Cobourg Peninsula.

Comments. Single carcass, in fresh condition, no external injuries, c. 2 m in length and weight 69 kg. Found 3 March by A. Withers, PWCNT. Collected entire by MAGNT and has been processed (Temporary taxonomy ref. no. 342) to be accessioned as a disarticulated skeleton.

Date. Stranded 28 October 2000.

Locality. 12°20'S, 130°53'E. Lee Point beach, Darwin.

Comments. Single carcass washed ashore in reasonably fresh condition, female, length 2.1 m. There were no obvious external injuries except a quite deep cut at the base of the tail, which is sometimes indicative of being caught in a mesh net. Thirty-one teeth in one maxillary row and 29 teeth in one mandible. Photographs (nos 6761-6756) and further measurements in PWCNT file P1999/629. Entire specimen collected by MAGNT; had not yet been registered at time of writing.

Tursiops truncatus cf. *aduncus* - bottlenose dolphin

Remarks. It is likely that all *Tursiops* in NT waters are referable to the subspecies *aduncus* (Banister *et al.*). This species group was under taxonomic review at the time of writing and *aduncus* may be elevated to full species rank in the future (C. Kemper, South Australian Museum, pers. comm.).

Date. Found 22 July 1972.

Locality. 14°53'S, 135°43'E. Maria Island, Gulf of Carpentaria.

Comments. Partially weathered skull, lacking mandibles, condylbasal length 420 mm, width 205 mm, height 160 mm; 25 (+?1) teeth alveoli in one maxillary row. Collected by D. Howe. No further details. Skull in the MAGNT, registered # U3955.

Date. Found 6 October 1972.

Locality. 11°00'S, 136°46'E. Cape Wessel, Marchinbar Island.

Comments. Partially weathered skull, lacking mandibles, condylbasal length 420 mm, width 210 mm and height 170 mm; 24 (+?1) teeth alveoli in one maxilla. Collected by W. Dodd. No further details. Skull in the MAGNT, registered # U3956.

Date. Found c. 1977 during the 'dry' season (May to September).

Locality. 11°47'S, 132°34'E. Mouth of Minimini Creek, south of Cobourg Peninsula.

Comments. Carcass of an adult, badly decomposed. Found by F. Woerle, PWCNT. Carcass left on site. No further details.

Date. Found 5 June 1985.

Locality. 11°26'S, 132°58'E. North-east of Murgella, Van Diemen Gulf.

Comments. Partially weathered skull, lacking mandibles, condylbasal length 430 mm, width 210 mm and height 160 mm; 24 teeth alveoli in one maxillary row. Collected by W. H. Butler, 5 June 1985. No further details. Skull in MAGNT, registered # U241.

Date. Found 30 November 1993.

Locality. 15°30'S, 136°57'E. Urquhart Island, Sir Edward Pellew Islands.

Comments. Bleached disarticulated skeleton, including skull and mandibles. Found by R. Chatto, 30 November 1993, lying among rocks. Condylbasal length of skull c. 420 mm, mandibular tooth count (from

alveoli) 24 + 24; wear on the only remaining tooth indicates animal was fully mature. Measured and photographed, but no material collected. Photographs (nos 5253-57) in PWCNT file P1999/629.

Date. Found 29 September 1994.

Locality. 15°30'S, 136°55'E. Pearce Islet, Sir Edward Pellew Islands.

Comments. Bleached skeleton, including skull and mandibles, found on beach by R. Chatto. Condylbasal length 400 mm; 22 (+2?) teeth alveoli in one maxillary row and one mandibular row on one side. Photographed and measured but no material collected. Photographs (nos 5284 and 87) in PWCNT file P1999/629.

Date. Found May 1998.

Locality. 12°24'S, 136°55'E. 10 km south of Cape Arnhem.

Comments. Weathered skull on beach; no other skeletal remains. Found by M. Stevens, PWCNT. Skull on display in the PWCNT office, Batchelor, NT.

Stenella attenuata - pan-tropical spotted dolphin

Date. Stranded, 20 October 1999.

Locality. 11°10'S, 132°09'E. Black Point, Cobourge Peninsula.

Comments. Single adult female 2.15 m in length stranded alive; emaciated. Examined same day by PWCNT staff and euthanased on veterinary advice. Field necropsy revealed old trauma to head, but no other obvious injuries. Histology of internal organs showed changes consistent with prolonged starvation, but no evidence of disease. Whole specimen secured near site for later retrieval of skeleton by MAGNT. Photographs and report in *NT News*, 6 November 1999. Photographs (nos 6536-54) and measurements in PWCNT file P1999/629.

Stenella longirostris - spinner dolphin

Date. Found 5 June 1985.

Locality. 11° 26'S, 132° 58'E. North-east of Murgencella, Van Diemen Gulf.

Comments. Weathered partial skull, lacking mandibles and maxillae; condylbasal length >370 mm, width 150 mm and height 130. Collected by W. H. Butler on 5 June 1985. No further details. Specimen compared with other *S. longirostris* skulls in MAGNT for identification. Skull in MAGNT, registered # U242.

Date. Stranded c.19 April 1994.

Locality. 11°17'S, 132°43'E. Templer Island, off Croker Island.

Comments. Single carcass, in fresh condition, no external injuries. Found by R. Chatto, 19 April 1994, on beach. Length of body 1.5 m, tip of upper jaw to apex of melon 150 mm, height of dorsal fin 150 mm; 43+ maxillary teeth and 45+ mandibular teeth on one side. No material collected. Photographs (nos 5240, 41, 45, 47, 49, and 51) in PWCNT file P1999/629.

Date. Found September 1998.

Locality. 11° 08'S, 132° 10'E. Just east of Smith Point, Cobourge Peninsula.

Comments. Five decomposing carcasses found by A. Withers, PWCNT, over a 30 m section of beach adjacent to a broad tidal flat with rapid tidal flux. Carcasses left on site. Single vertebra collected for display at Black Point Ranger Station, Gurig National Park. No further details

Peponocephala electra - melon-headed whale

Date. Stranded, from 21 to 26 March 1996.

Locality. 11°45'S, 135°54'E. Eastern end of Elcho Island.

Comments. A mass stranding of 40 animals, occurred over six days. Examined and photographed by R. Chatto; one complete skull collected, condylbasal length 440 mm, width 250 and height 190 mm; 25 teeth alveoli in one maxillary row and 24 teeth alveoli in one mandibular row. Photographs (nos 4775, 77-79, 80, 82-85 and 91) in PWCNT file P1999/629. Complete skull in MAGNT, registered # U4438. See Chatto (2000c) for a detailed description.

Date. Found 8 October 1996.

Locality. 15°35'S, 136°31'E. North-west side of West Island, Sir Edward Pellew Islands.

Comments. Weathered skull, lacking mandibles, found on beach by R. Chatto. Condylbasal length 300 mm, width 200 mm, 19+ teeth alveoli on either side. Photographed and measured but no material collected. Photographs (nos 5264 and 75) in PWCNT file P1999/629. Identification confirmed with reference to MAGNT # U4438.

Pseudorca crassidens - false killer whale

Date. Found 1968.

Locality. 11°13'S, 131°59'E. Trepan Bay, Cobourge Peninsula.

Comments. Bleached skull and mandibles, condylbasal length 620 mm, width 350 mm and height 260 mm; nine teeth in each maxillary row, eight in each mandible. Collected by H. J. Frith, CSIRO. No further details. Skull and mandibles in the Museum and Art Galleries of the Northern Territory (MAGNT), registered # U2056.

Date. Found 8 October 1996.

Locality. 15°35'S, 136°31'E. North-west side of West Island, Sir Edward Pellew Islands.

Comments. Weathered skull, lacking mandibles, found on beach by R. Chatto. Condylbasal length 560 mm, width 330 mm, height 260 mm, c. 9-10 pairs of teeth in each jaw. Photographed and measured, but no material collected. Photographs (nos 5267, 69, 71-72) in PWCNT file P1999/629.

***Globicephala macrorhynchus* - short-finned pilot whale**

Date. Stranded 18 March 1999.

Locality. 11°11'S, 130°22'E. Cape Van Diemen, NE tip of Melville Island.

Comments. Three adults and two juveniles on beach, reported by Coastwatch. When examined next day by R. Chatto, only the smallest was still alive. It was euthanased and all specimens were left on site. Reported in *NT News*, 19 March 1999. Photographs (nos 5798-5804) in PWCNT file P1999/629. See Chatto (2000d) for a detailed description.

***Globicephala* sp. - pilot whale**

Date. Found 1983.

Locality. 12°05'S, 135°22'E. Jigaimarea Point, Howard Island, NW Arnhem Land.

Comments. A school of 30-50 ashore. Source of report not stated, no further details. NCSD # 168.

Date. Found 1984.

Locality. 12°02'S, 134°58'E. Yabooma Island, off Millingimbi, NE Arnhem Land.

Comments. A school of 20 animals reported to have stranded - one died and the remainder escaped. Source of report not stated, no further details. NCSD # 169.

Date. Found 1984.

Locality. 12°02'S, 134°58'E. Yabooma Island, off Millingimbi, NE Arnhem Land.

Comments. Three animals reported to have stranded - one died and two escaped. Source of report not stated, no further details. NCSD # 170.

Date. Stranded c. 31 March 1985.

Locality. 15°24'S, 136°13'E. Rosie Creek, SW Gulf of Carpentaria.

Comments. Group of eight animals seen on 1 April 1985 comprising six adults and two calves; one large male still alive. Some whales on beach, some above high tide mark and some washed inland of tree line by cyclone surge. Source of report not stated, no further details. NCSD # 173.

Date. Found 10 April 1985.

Locality. 16°04'S, 137°17'E. Myoorlka Island, mouth of the Robinson River, SW Gulf of Carpentaria.

Comments. Single animal on beach, partly covered by sand and weed. Source of report not stated, no further details. NCSD # 174.

***Orcaella brevirostris* - Irrawaddy dolphin**

Date. Found 16 July 1948.

Locality. 12°15'S, 136°41'E. Melville Bay, near Gove.

Comments. Johnson (1964) reports two skulls of unknown sex, one with a partial body skeleton, were picked up at an Aboriginal campsite during the American-Australian scientific expedition to Arnhem Land. The skulls were likely to have been the remains

of dolphins eaten by Aborigines and caught in Melville Bay. Photographs and some skull measurements are given in Johnson (1964).

Date. Found 12 June 1992.

Locality. 12°50'S, 130°16'E. Fog Bay, 70 km SW of Darwin.

Comments. Single carcass, decomposing, c. 1.5 m in length, with bulbous head partly eaten by dingos. Found and examined by R. Chatto. No material collected. Photographs in PWCNT file P1999/629.

Date. Found August 1997.

Locality. 12°37'S, 130°31'E. Indian Island, Bynoe Harbour.

Comments. Weathered skull on beach, no other skeletal remains. Collected by PWCNT staff. Skull on display in the PWCNT Office, Batchelor, NT.

Date. Found 27 May 1999.

Locality. 13°22'S, 136°08'E. North-east side of Isle Woodah, Gulf of Carpentaria.

Comments. Collapsed and dehydrated carcass, skin and flippers still present, body length estimated 1.5 m. Skull separate, clean, mandibles lacking, 18 tooth alveoli in each maxilla. Found by R. Chatto, no material collected. Photographs (nos 6110 and 6111) in PWCNT file P1999/629.

Date. Stranded 1 October 1999.

Locality. 12°46'S, 130°22'E. Dundee Beach, Fog Bay.

Comments. Single adult female 1.93 m in length, washed ashore dead. Examined same day by PWCNT staff; six 5 cm cuts in a line along its belly. These were likely to have been done by a person with a knife, probably after death to cause the animal, which may have been removed from a fishing net, to sink. Estimated to have died 1-2 days previously. Necropsy indicated that the animal was healthy and in good condition prior to death. Specimen currently held frozen by MAGNT (Temporary taxidermy ref. no. 1366) to be accessioned as a disarticulated skeleton. Photographs (nos 6409-14) and measurements in PWCNT file P1999/629.

Dolphin, unidentified

Date. Found June 1983.

Locality. 13°06'S, 130°07'E. Just north of Channel Point, opposite North Peron Island.

Comments. Partly decomposed carcass lying in intertidal zone, estimated length c. 2.5 m. Found by A. Donati, Department of Primary Industries and Fisheries (DPIF). Specimen left at site, no further details.

Date. Stranded 13 April 1985.

Locality. 13° 50'S, 136° 00'E. South of Cape Barrow, west of Groote Eylandt.

Comments. Found alive, but rescue not attempted. Possibly *Tursiops* but definitive details not recorded. NCSD # 175.

Date. Found 17 May 1985.

Locality. 13°39'S, 129°48'E. c.17 km south of Cape Scott, 160 km SW of Darwin.

Comments. One animal ashore and a second floating near shore c. 2 km to west. Source of report not stated, no further details. NCSD # 179.

Family Ziphiidae

Ziphius cavirostris

Cuvier's or goose-beaked whale

Date. Found 1969.

Locality. 11°22'S, 132°18'E. Cobourg Peninsula.

Comments. Weathered skull, lacking mandibles, condylobasal length 910 mm, width 480 mm and height 500 mm. Collected by D. Lindner, PWCNT. No further details. Photographs in PWCNT file P1999/629; skull in MAGNT, registered # U2055.

Date. Found 30 July 1998.

Locality. 12°02'S, 134°57'E. Yabooma Island, off Millingimbi.

Comments. Bleached skeletal remains including skull, lacking mandibles, found high on beach adjacent to low shrubs by R. Chatto. Condylobasal length c. 1000 mm, width c. 500 mm, height c. 400 mm; c. 3 m portion of vertebral column lying in situ. Photographed and a single vertebra collected; retained in Darwin office of PWCNT. Photographs (nos 5499, 5500 and 5501) in PWCNT file P1999/629. Identified by G. J. B. Ross, who commented that it was probably a mature female, based on fusion of the epiphyses to the centra of the vertebrae and on skull characters. Skull collected by R. Chatto on 18 November, 2000; deposited at MAGNT (not registered at time of writing).

Beaked whale, probably *Ziphius cavirostris*

Date. Found 2 August 1984.

Locality. 12°03'S, 134°55'E. A small island (possibly called Rakuna), just south of Yabooma Island off Millingimbi.

Comments. Single animal, length 5.18 m stranded alive but date uncertain. Reported by the Northern Land Council to PWCNT. When examined by P. Whitehead, PWCNT, on 2 August, the carcass had decomposed to the point where the skull and mandibles were 'clean' except for some skin at the very tip; no sign of erupted teeth or alveoli and deterioration of the genital/anal area precluded determination of sex. Specimen photographed and measured, but no necropsy was performed and no material was collected because of the totemic significance of the animal to the Aboriginal traditional owners. Those who saw the whale alive identified it as *Z. cavirostris* with reference to the illustration of the Indo-Pacific form in Watson (1981: 118). Measurements and five photographs (un-numbered) on PWCNT file P1999/629. NCSD # 31.

Family Physeteridae

Physeter macrocephalus - sperm whale

Date. Stranded c.17 November 1980.

Locality. 11°39'S, 133°22'E. Off north-west side of South Goulburn Island, on a reef c. 2 km offshore.

Comments. Freshly dead when found by a fisherman on 18 November 1980. Lodged among mangroves on South Goulburn Island when investigated by MAGNT staff on 24 November 1980, estimated length 13 m. Reduced to a skeleton by late December. Substances from rotting carcass had killed the mangroves over a radius of 100 m (I. Archibald, MAGNT, pers. comm.). Aboriginal traditional owners would not allow any part of the specimen to be collected. NCSD # 166. See also Hodgkinson (1987) for further details regarding the Aboriginal issues concerning the stranding.

Date. Stranded c. 1987.

Locality. 14°13'S, 129°25'E. Beach near Port Keats.

Comments. Bleached skull observed from aircraft by R. Chatto, 15 December 1992. Advised by Sgt. Kevin Winzar of Port Keats police that the whale washed 9 km to the NNW about 1987. It was not examined and was left to disintegrate on site. Sgt. Winzar photographed the skull on 17 December 1992 and measured the width at 120 cm and height at 70 cm. No further details. Photographs in PWCNT file P1999/629.

Date. Stranded 22 January 1993.

Locality. 12°21'S, 130°52'E. Casuarina Beach, Darwin.

Comments. Single, adult male stranded alive, 15.4 m in length. Grounded in shallows and died soon after. Skeleton collected for display by MAGNT (file BP2000/793); not registered in scientific collection. Photographs and report in *NT News*, 23 January, pp 1,14,15. See also Chatto (2000a) for more detailed description.

Date. Stranded between 3 and 6 August 2000.

Locality. 11°34'S, 133°05'E. 1 km south of Brodgen Point, east of Murgena.

Comments. Freshly dead male lying in the intertidal zone, length c. 15 m. Found by P. Luton, PWCNT, on 6 August 2000. It had not been there on 3 August 2000. Examined and photographed by R. Chatto on 17 August 2000; no external injuries; 24+ teeth in one mandibular row, several broken. Carcass left on site. Site revisited by R. Chatto on 17 November, 2000. Skull (minus all teeth), some vertebrae and a rib bone still present. Additional measurements and photographs taken, and rib collected and deposited in MAGNT (not yet registered at time of writing). Photographs (nos 6742-48 and 6844-52) and measurements in PWCNT file P1999/629.

Family Kogiidae

Kogia simus - dwarf sperm whale

Date. Stranded 19 August 1995.

Locality. 12°22'S, 130°51'E. Nightcliff Beach, Darwin.

Comments. Adult male, length 2.1 m, stranded alive late afternoon. Towed out to sea and released. Stranded next day on Mindil Beach, where it died during rescue attempts. Photographs and report in *NT News*, 21 August 1995, p 1. Necropsy performed, photographs and measurements taken; details in PWCNT file P1999/629. Specimen currently in MAGNT freezer (Temporary taxidermy ref. no. 126); to be accessioned as a disarticulated skeleton. See Chatto (2000b) for a detailed description.

Family Balaenopteridae
***Balaenoptera musculus* - blue whale**

Date. Found 19 December 1980.

Locality. 12°04'S, 131°18'E. Beach on the east side of Cape Hotham.

Comments. Specimen in skeletal condition, estimated length c. 25 m. Found by a fisherman who removed and sold some vertebrae as garden seats. Remainder of skeleton collected by MAGNT staff some months later and put on public display at MAGNT; not registered in scientific collection. Identification confirmed by S. Van Dyck, Queensland Museum, on the basis of skull measurements. NCSD # 165.

***Megaptera novaeangliae* - humpback whale**

Date. Found 1981.

Locality. 11° 59'S, 135° 49'E. Napier Peninsula, NE Arnhem Land.

Comments. Found dead with a hole in its side, estimated length 10 m. Source of report not stated, no further details. NCSD # 167.

***Balaenoptera* sp.**

Date. Stranded January 1996.

Locality. 13°10'S, 136°17'E. Western point of entrance to Myoola Bay, Gulf of Carpentaria.

Comments. Carcass washed ashore, estimated length 10+ m. Found February 1 and photographed by Waka, an Aboriginal traditional owner from the Banyalla community. Carcass lodged near mangroves in an advanced state of decomposition, but numerous throat grooves still evident. R. Chatto visited site with Waka in May 1999, at high tide, but no remains could be seen. No further details. Photograph in PWCNT file P1999/629.

Date. Stranded c. 19 April 1999.

Locality. 12°24'S, 136°55'E. 15 km south of Cape Arnhem, near Gove.

Comments. Decomposed carcass, estimated length 10+ m washed ashore on or just before 19 April 1999. Dhimurru Land Management Aboriginal Corporation provided photographs and video taken 10 May 1999, which show a flipper of moderate length, numerous throat grooves and the skull missing. Remains left on site, and were still present but very decomposed when

examined and photographed by R. Chatto on 27 May 1999. No further details. Photographs (nos 6117-6120) in PWCNT file P1999/629, copy of video in Darwin office of PWCNT.

Family and species unknown

Date. Found February 1984.

Locality. 15°40'S, 137°00'E. Vanderlin Island, Sir Edward Pellew Islands.

Comments. A group of six whales ashore. Reported by Coastwatch whose observers supposed that they could have been driven ashore by cyclone 'Kathy'. No further details.

Date. Stranded 1 August 1984.

Locality. 12°02'S, 134°56'E. Yabooma Island off Millingimbi.

Comments. Alive when seen by Coastwatch; length estimated at 4.5 m. Coastwatch observers commented that the weather was rough at the time and described the whale as black with white marks on the head, a colour pattern suggestive of *Z. cavirostris*. No further details. NCSD # 171.

Date. Found April 1985.

Locality. 15°36'S, 137°10'E. 2 nautical miles SSE of Cape Vanderlin, Sir Edward Pellew Islands.

Comments. Two animals, possibly a mother and calf. Observer in aircraft thought they were too large for dolphins. Source of report not stated, no further details. NCSD # 172.

Date. Found 16 April 1985.

Locality. 15°02'S, 135°34'E. North of mouth of Limmen River, Gulf of Carpentaria.

Comments. Single animal on beach, dead. Reported by Coastwatch. No further details. NCSD # 176.

Date. Found 16 April 1985.

Locality. 15°36'S, 136°33'E. West Island, Sir Edward Pellew Islands.

Comments. At least one animal on beach, dead. Reported by Coastwatch. No further details. NCSD # 177.

Date. Found 1985 during 'dry' season (May to September).

Locality. 11°20'S, 132°56'E. Just east of De Courcy Head, north of Murgarella.

Comments. Decomposing carcass, estimated length 5 m. Observed from aircraft by A. Donati, DPIF. No further details.

Date. Found 9 May 1985.

Locality. 16°00'S, 137°12'E. 2 nautical miles north of Robinson River mouth, SW Gulf of Carpentaria.

Comments. Single animal, decomposing, estimated dead for 2-3 weeks. Length said to be approximately 6-7 m. Reported by Coastwatch, who said it appeared to be unlike *Globicephala* and was possibly a baleen whale. However, this is very small for such. No further details. NCSD # 178.

Date. Found pre 1990.

Locality. 12°54'S, 130°20'E. Just south of Finniss River mouth.

Comments. Skeletal remains of large whale, one rib c. 3 m in length, possibly either a large *Physeter* or a large baleen whale. Reported to R. Chatto in June 1999 by Aboriginal traditional owner. No further details.

Date. Found early 1990s, in month of February.

Locality. 12°13'S, 136°15'E. North-east part of Arnhem Bay.

Comments. Bleached skeletal remains of a whale c. 5 m in length, but possibly longer. Observed from aircraft by M. Stevens, PWCNT. Reported to R. Chatto, June 1999. No further details.

Date. Stranded December 1994.

Locality. 11° 57'S, 134° 10'E. West Point, near Maningrida.

Comments. Large individual washed ashore, left untouched. Reported to R. Chatto by Northern Land Council in 1995. Site visited by R. Chatto on 17 November, 2000. One mandible (no teeth alveoli; curved length 2.97 m), on vertebra and two ribs remaining. The specimen can now be confirmed as a baleen whale. The vertebra was collected and deposited in MAGNT; not yet registered at time of writing. Photographs (nos 6866-72) and measurements in PWCNT file P1999/629.

Date. Stranded January 1998.

Locality. 11°02'S, 132°35'E. North-east side of Croker Island.

Comments. Five small black whales stranded on beach; four c. 1.5 m and one c. 1.0 m in length. Report by Aboriginal traditional owners via Northern Land Council to R. Chatto stated that the animals "had a dorsal fin but a blunt nose, not like normal dolphins". Two were returned to the sea but the others persistently re-stranded, and were left on site. One had cuts to the belly area. No further details.

DISCUSSION

There is scant information on the occurrence of cetaceans in NT waters. This unsatisfactory situation is the result of many factors, including the remoteness of much of the Territory's coastline, the sparse and non-randomly distributed human population, the sporadic nature of human activity in inshore waters, poor communication, historical disinterest and continuing low levels of scientific inquiry. These latter two issues are due in part to the cost and logistical difficulties of survey and salvaging specimens from remote areas.

Thus when Bannister *et al.* (1996) prepared the first comprehensive review of Australia's cetaceans, they could confidently list for the Northern Territory only 12 (inclusion of *Mesoplodon layardii* in their Table 1 is an error) of the 26 species known to occur in Australia's tropical waters. They provisionally included two others on the basis of uncertain identification of specimen

material. Records based on strandings, accumulated from a variety of sources and summarised here, include ten of those 12 species, while the two provisionally included (*Globicephala macrorhynchus*, *Kogia simus*), are now confirmed. The melon-headed whale *Peponocephala electra*, can now also be added to the Northern Territory list. Two species listed from the NT by Bannister *et al.* (1996), but yet to be recorded by strandings are the rough-toothed dolphin *Steno brenadensis* and common dolphin *Delphinus delphis*.

In addition, another species can now be confirmed for NT waters and an additional species to Commonwealth waters off the NT coast. Confirmation of the killer whale, *Orcinus orca*, in NT waters is based on a sighting made on 7 April 1999 at Yirrkala (12° 15'S, 136° 54'E) by C. Lane, and reported by the Dhimurru Land Management Aboriginal Corporation. At least one animal was seen from shore at around 12.30 h approximately 1 km out to sea and heading south. The animal was described as 3-4 times the size of a dolphin, strikingly marked with black on top and white below, and with a very large dorsal fin. (The dolphins most frequently seen in this area are *Sousa chinensis* and *Tursiops truncatus* cf. *aduncus*, i.e. individuals about 2.5 m in length (Chatto, pers. obs.)) One old Aboriginal lady said that she had not seen this species for 20 years, but does remember seeing them from time to time when her children were young. Confirmation of the sei whale, *Balaenoptera borealis*, in Commonwealth waters off the NT coast is based on a sample of baleen from a dead specimen c. 15 m in length, trawled up from 113 m by a Thai fishing vessel on 1 September 1989 at 10° 21'S, 133° 55'E, approximately 160 kilometres north-east of Croker Island. The specimen of baleen was donated to MAGNT where it is on display but it has not been registered in the scientific collection.

Of the total series of 57 stranding events reported on here (Table 1), 35 were identifiable to species, seven to genus (*Globicephala*, *Balaenoptera*), and the remainder could be described only as 'dolphin' (3), 'beaked whale' (1) or 'unknown' (11).

This series is too small and the data available for most events too meagre for intra- and inter-species comparisons. Similarly, there are too many confounding factors and biases to search for any patterns in geographic distribution of the 57 events. For instance, there is no way of telling whether any of the singletons found dead were alive when they beached, or if they died at sea and their floating carcasses had been transported by current, wind and tide over considerable distances before they eventually washed ashore.

However, it is appropriate to consider the results of this study in terms of the known distributions of these 13 species and their habitat preferences, seasonal movements or migrations. We have grouped them according to broad oceanographic categories based on

Table 1. Species, number of stranding events and number of individuals per event

Species	Common name	No. of stranding events	No. of individuals per event
<i>Balaenoptera musculus</i>	blue whale	1	1
<i>Balaenoptera</i> sp.	baleen whale sp.	2	1 (x2)
<i>Globicephala macrorhynchus</i>	short-finned pilot whale	1	5
<i>Globicephala</i> sp.	pilot whale sp.	5	1, 3, 8, 20, 30-50
<i>Kogia sima</i>	dwarf sperm whale	1	1
<i>Megaptera novaeangliae</i>	humpback whale	1	1
<i>Orcaella brevirostris</i>	Irrawaddy dolphin	5	1 (x4), 2
<i>Peponocephala electra</i>	melon-headed whale	2	1, 40
<i>Physeter macrocephalus</i>	sperm whale	4	1 (x4)
<i>Pseudorca crassidens</i>	false killer whale	2	1 (x2)
<i>Sousa chinensis</i>	Indo-Pacific hump-backed dolphin	5	1 (x 4), 3
<i>Stenella attenuata</i>	pan-tropical spotted dolphin	1	1
<i>Stenella longirostris</i>	spinner dolphin	3	1, 1, 5
<i>Tursiops truncatus</i> cf. <i>aduncus</i>	bottlenose dolphin	7	1 (x 7)
<i>Ziphius cavirostris</i>	Cuvier's beaked whale	2	1 (x2)
'beaked whale'	beaked whale sp.	1	1
'dolphin'	dolphin sp.	3	1 (x3)
'unknown cetacean'	unknown cetacean sp.	11	1 (x7), 1+, 2, 5, 6

water temperature and commonly used to define distributions, as follows.

Tropical – subtropical. Includes two inshore species (Indo-Pacific hump-backed dolphin and Irrawaddy dolphin), and two offshore species (melon-headed whale and the spinner dolphin), both of which range into coastal waters.

The Indo-Pacific hump-backed dolphin is restricted to coastal, inshore and estuarine habitats throughout northern Australia, ranging south along the WA coast to about 24°S, and to Moreton Bay in Queensland, at 27°30'S (Bannister *et al.* 1996). Stragglers have been recorded as far south as Sydney (Llewellyn *et al.* 1994). This species is not known to be migratory, but individuals may move about a great deal along-shore and between islands. It appears to be loosely social in small groups (Ross *et al.* 1994) and is not prone to strand. This species is often seen in very shallow water in large tidal variation areas and does not become stranded (Chatto pers. obs.). G. Ross (pers. comm.) has also seen this species school fish up onto sandbanks and then slide up to grab them without becoming stuck. Thus all five NT records listed here probably represent mortality at sea rather than active strandings.

The Irrawaddy dolphin has a similar but slightly more restricted distribution in northern Australia, occurring on the WA coast north of Broome (18° S), throughout the NT and to Gladstone (23° 50'S) on the Queensland coast (Banister *et al.* 1996). It is usually encountered in groups of less than 6 animals, but groups of 10-15 animals have been reported (Marsh *et al.* 1989). As this species is not prone to strand, the five NT records listed here probably also represent mortality at sea.

The spinner dolphin inhabiting NT waters has recently been described as a subspecies – *Stenella*

longirostris roseiventris (Perrin *et al.* 1999). It is a small form restricted to the shallow inner waters of South-east Asia, including the Gulf of Thailand, Timor and Arafura Seas, and similar waters of Indonesia, Malaysia and northern Australia; it is not known to be migratory. In deeper oceanic waters it is replaced by the typical and larger pelagic form, *S. l. longirostris* (Perrin and Gilpatrick 1994). Little is known of the occurrence of spinner dolphins in northern Australia, even though they were commonly caught by accident in the Taiwanese gillnet fishery for sharks in the Timor and Arafura Seas (Harwood and Hembree 1987). *Stenella l. roseiventris* is known, however, to feed on shallow water benthic and reef dwelling fish, squid, cuttlefish and shrimp (G. Hembree, cited in Perrin *et al.* 1999). More southern records, to Bunbury in WA (30°19'S, Bannister *et al.* 1996), from the Great Barrier Reef and in NSW to Uranga (30°31'S, Llewellyn *et al.* 1994) appear to be of the pelagic form. The close grouping of the three NT records listed here over less than 1 degree of longitude, and including a mass stranding, may indicate a centre of activity for *S. l. roseiventris* in that region, as there is no reason to suspect it may be attributable to greater observer activity.

The melon-headed whale is a highly social deep-water species, occurring in large schools and often associated with other oceanic dolphins and small whales (Leatherwood and Reeves 1983; Perryman *et al.* 1994). Schools have been sighted over the continental slope off northern NSW (Dawbin *et al.* 1970) and several mass strandings have occurred in southern Queensland (Bryden *et al.* 1997) and NSW (Dawbin *et al.* 1970; Smith 1997). The small school that stranded on Elcho Island in the NT in 1996 may have become disorientated when navigating in unfamiliar shallows, however little is known about

this species which may not be restricted to deep waters only (Ross pers. comm.).

Tropical – temperate. Four ecologically very different species fit this general category – pan-tropical spotted dolphin, bottlenose dolphin, false killer whale and dwarf sperm whale.

The spotted dolphin occurs circumglobally in deep offshore waters, most frequently where sea surface temperatures exceed 25° C and overlie a sharp thermocline at depths less than 50 m (Perrin and Hohn 1994). It is often encountered in large schools and is often associated with spinner dolphins. In Australia, spotted dolphins are known to occur north of Augusta in WA (38° 20'S) and north of Sydney on the east coast (34° 00'S, Bannister *et al.* 1996). Their activity patterns in Australian waters are not known, but elsewhere, seasonal inshore-offshore movements occur in spring (Leatherwood and Reeves 1983). The timing of the one NT record of a compromised adult fits this pattern.

The *aduncus* form of bottlenose dolphin is very widely distributed in tropical, subtropical and temperate Australian waters, ranging south to about 32° S. Where it occurs sympatrically with the hump-backed dolphin it tends to be active slightly further offshore, but often in depths of less than 10 m, and may range to about 10 km beyond the shelf (Bannister *et al.* 1996). Because bottlenose dolphins navigate confidently in shallow and confined waters, the seven NT records, all singleton events, probably represent mortality at sea. This appears to be the case with the typical *truncatus* form in Victoria where many events involve aged, diseased, injured and very young animals (Warneke, unpublished data).

The false killer whale is an oceanic species, rarely approaching land except where the continental shelf is narrow. In Australia, false killers have been widely recorded by some sightings and strandings in all states. Strandings occur throughout the year, but the majority of mass events occur from May to September on south and south-east coasts, indicating a seasonal movement inshore or along the continental shelf (Bannister *et al.* 1996), possibly associated with abundances of prey. The two singleton events in the NT are unrevealing, but probably represent mortality at sea.

The short-finned pilot whale occurs throughout tropical and warm temperate regions of Indian, Pacific and Atlantic Oceans, but the southern limits of its range are poorly known, partly because of the difficulty of distinguishing it from the closely similar long-finned pilot whale, *Globicephala melas*, at sea. The short-finned pilot whale appears to be widely distributed off Australia's northern coast where it ranges into continental seas. Records from temperate waters on the southern coast (South Australia, Tasmania) probably reflect the influence of the south-flowing, warm Leeuwin Current and/or East Australia Current (Bannister *et al.* 1996). Because *G. melas* is restricted to temperate waters

(the most northern record in Australia is of a straggler at Point Lookout in Qld (27° 26'S, Paterson 1986) it is reasonable to assume that the five NT 'pilot whale' records are of this species, making six in total. The high proportion of school strandings (5) in this series and their wide geographic spread indicate considerable activity in NT waters and that this species is at high risk when navigating near the shore in those areas. The large and fast tidal variations of the NT may also be influential in this regard.

The dwarf sperm whale is primarily oceanic and occurs world wide within about 40° N and S of the equator. The frequency and distribution of strandings in some regions appears to correlate with continental shelf width and important current systems, and suggests that the species might be more abundant in the warmer parts of its range (Caldwell and Caldwell 1989). It feeds primarily on benthic and demersal organisms. Dietary studies in southern Africa (Ross 1984) indicate that juveniles and immatures are active over the outer continental shelf and slope where suitable prey is often more abundant and that adults feed in deeper waters beyond the shelf. Comparative data suggest that dwarf sperm whale is more active nearer to coasts than the pygmy sperm whale, *Kogia breviceps*, but in Australia the former strands very rarely by comparison, with single records only in WA, SA, NSW and now the NT.

Tropical – subantarctic. Cuvier's beaked whale occurs world-wide within this broad latitudinal range. It is a true oceanic species, normally ranging far from land. It is thought to be resident in some areas, e.g. off Japan, where it is most common in waters deeper than 1000 m (Nishiwaki and Oguro 1972). In the Australian region it is known from a few strandings in all mainland states, but many more (15) in Tasmania (Bannister *et al.* 1996). Strandings have been recorded in all months except September to January, but this indication of seasonality of occurrence may be an artefact of the small series of just 12 dateable events. No pattern of seasonality has been detected in strandings elsewhere (Heyning 1989). The two certain and one probable NT events listed here suggest that the species is not uncommon in the region, but otherwise are unrevealing.

Tropical – Antarctic. Sperm whales range widely in all oceans and tend to concentrate in the vicinity of steep continental shelves, oceanic islands and sea mounts where favoured prey are more abundant. Breeding females form stable nursery schools, while adult males are solitary or associate in temporary bachelor schools. Judging by the frequency of strandings, sperm whales are common in Australian waters. The majority of events have occurred in the south-east and most involved single animals, 75% of which were male. In striking contrast mass strandings are rare, except in Tasmania (15 events, Warneke, unpublished data). The series shows a strong seasonal bias, with most singleton events occurring in

spring to autumn, and mass events in January – March, September and October. While this pattern accords with the known generalised open ocean movement of the species southwards in summer (Rice 1989; Bannister *et al.* 1996), very little is known of its activities near-shore. The four NT singleton events listed here of known date indicate that sperm whales, probably only adult males, are present in the region during summer.

Two forms of blue whale are recognised – the world wide ‘true’ blue, *Balaenoptera musculus intermedia*, and the southern hemisphere pygmy blue, *B. m. breviceauda*, which is most abundant in the Indian Ocean (Yochem and Leatherwood 1985). Both forms migrate between warm water breeding grounds at low latitudes and cold water feeding grounds at high latitudes – the blue penetrating to the Antarctic ice edge, whereas the pygmy blue normally feeds north of 55° S. In recent years blue whales have been encountered relatively close to the Australian coast at various places, mainly in southern waters from Rottnest Island WA to southern NSW; the most northern records being sightings off the Dampier Archipelago in WA at about 20° S (Bannister *et al.* 1996) and a stranding at Couti Uti in Qld (22°20’ S, Paterson 1986). The single confirmed record for the NT extends the known range in the Australian region by 8 degrees of latitude. At the time this paper was going to print, a 21 m blue whale washed up dead on to Troughton Island (13°45’ S, 126°09’ E) in NW Western Australia on November 7, 2000 (Chatto pers. obs.).

Two relatively discrete Australian populations of humpbacked whales undertake a seasonal north-south migration similar to that of the blue whale, but between breeding grounds on either side of the continent at about 15–20° S and feeding grounds at about 60–70° S; some individuals may remain in the tropics, e.g. in Torres Strait (Bannister *et al.* 1996). Migrating animals generally pass close to the coast at various points, and stragglers may enter bays and inlets where they navigate confidently in confined shallow waters, e.g. in Victoria (Warneke 1995a). Consequently strandings are rare and apart from live animals entangled in netting they almost invariably involve individuals that have died at sea from natural causes. The NT stranding appears to be one such natural event.

Other species likely to strand in the Northern Territory. Finally, it remains to consider what species might in future strand in NT waters and to emphasise the importance of investigating as many events as possible to obtain authentic identifications and to document little known aspects of the species’ biology. Bannister *et al.* (1996) lists 14 species that are widely distributed in the tropical region and are likely to range into the tropical waters of the Australian region, but which have not been authentically recorded in the NT. We provide brief comment on each of these, as well as

the rough-toothed dolphin, killer whale and Bryde’s whale not included in the review above.

The rough-toothed dolphin, *Steno bredanensis*, is widely distributed in deep offshore waters in tropical to warm temperate latitudes, including the Indo-Australian Archipelago, but it is not known to be numerous. It is social and gregarious, and associates with pilot whales and bottlenose dolphins (Leatherwood and Reeves 1983). It was listed for the NT by Bannister *et al.* (1996).

Risso’s dolphin, *Grampus griseus*, is abundant and cosmopolitan in tropical to warm temperate waters (Leatherwood and Reeves 1983) and although an oceanic species it is frequently seen over the continental slope and ranges onto the shelf in parts of Australia (e.g. Corkeron and Bryden 1992).

The striped dolphin, *Stenella coeruleoalba*, is widely distributed in deep waters in tropical to warm temperate latitudes, ranging to the outer edge of the continental slope. It is social and gregarious, and is known to be migratory in some regions (Perrin *et al.* 1994). In Australia, southernmost records are strandings and may be related to the south-flowing warm Leeuwin and East Australia Currents – at Augusta WA (34° 20’ S, Bannister *et al.* 1996) and at Woolongong NSW (34° 23’ S, Llewellyn *et al.* 1994).

The common dolphin, *Delphinus delphis*, is very widely distributed and abundant in tropical to temperate latitudes, but there are very few records from Australian tropical waters (Bannister *et al.* 1996), which may reflect its preference for areas of high topographical relief and upwellings (Evans 1994) and the very wide continental shelf around northern Australia. The species is often encountered over the narrow continental shelf in south-eastern Australia, where many singleton strandings have been recorded (Nicol 1987; Kemper and Ling 1991; Warneke 1995b); mass strandings are rare, except in Tasmania. The species *Delphinus tropicalis* is more likely to occur in waters off the NT coast than *D. delphis* (Ross pers. comm.).

Fraser’s dolphin, *Lagenodelphis hosei*, is abundant and widely distributed in oceanic tropical waters (Perrin, Leatherwood and Collet 1994) and could be expected in waters off the NT coast (Ross pers. comm.). This species occasionally strays into temperate regions, where single and mass strandings have occurred, e.g. in NSW (Llewellyn *et al.* 1994) and Victoria (Warneke 1995c).

The pygmy killer whale, *Feresa attenuata*, is primarily tropical in distribution; records from higher latitudes being associated with warm boundary currents (Ross and Leatherwood 1994). In Australia it is known from sightings in north-eastern waters and several strandings in NSW (Llewellyn *et al.* 1994) and WA (Bannister *et al.* 1996).

The killer whale, *Orcinus orca*, is cosmopolitan, occurring from the equator to polar seas. In Australia

this species is often seen along the continental slope and on the shelf, and has been recorded from all states, but more commonly in the southern waters (Bannister *et al.* 1996). Killer whales navigate confidently in very shallow waters, consequently live strandings are rare. Several singleton events in Victoria and Tasmania involved very old and juvenile individuals and one neonate that had died at sea, or were moribund when they beached (Warneke, unpublished data), ie they were instances of natural mortality. Similar events can be expected in the NT.

Longman's beaked whale, *Indopacetus pacificus* (Moore 1968) (= *Mesoplodon pacificus* Longman 1926), is known only from two skulls, one from Mackay, Qld, at 21°09'S and the other from Danane, just north of the equator in Somalia – points which suggest an Indo-Pacific distribution. At an estimated length of c. 7.5 m it is by far the largest mesoplodontid. Intriguingly during the past three decades there have been numerous sightings of large beaked whales very similar in form to the southern bottlenose whale *Hyperoodon planifrons* (see below), in tropical waters of the Indian and Pacific Oceans. A recent review of these sightings and some associated photographs by Pitman *et al.* (1999) indicates that this 'tropical bottlenose whale' differs from *H. planifrons* in several respects and that it is almost certainly the elusive *I. pacificus*. Any report of a large beaked whale stranded in the NT should be promptly investigated.

Blainville's beaked whale, *Mesoplodon densirostris*, is an oceanic species widely distributed in tropical to temperate waters world wide. In Australia it is known only from strandings, in most of the southern states and from WA and Qld south of 20° 10'S (Mead 1989). Records in NSW, Victoria and on the west coast of Tasmania may be of stragglers ranging southwards in the warm Leeuwin and East Australia Currents.

The southern bottlenose whale, *Hyperoodon planifrons*, is included here only on the basis of the proximity of a record (the type specimen) from Lewis Island in the Dampier Archipelago (20° 35'S) in WA. The normal range of this species is considered to be south of 30° S to the Antarctic ice edge (Bannister *et al.* 1996). Although commonly and widely encountered in deep oceanic waters (Ross 1984) this species appears to avoid continental seas and strands infrequently (Baker 1983).

The pygmy sperm whale, *Kogia breviceps*, has a similar world wide distribution to its congener *K. simus*, but tends to remain in deeper waters further offshore (Caldwell and Caldwell 1989). However, in Australia *K. breviceps* strands much more frequently and most records are concentrated on the east and south-east coasts, especially in NSW (38 records to 1992, Llewellyn *et al.* 1994), possibly because of the relatively narrow continental shelf in much of that region.

Two rorquals – minke whale, *Balaenoptera acutorostrata*, and Bryde's whale, *B. edeni*, are known from tropical waters. In the Australian region their status and movements are not well understood, and the situation is further complicated by the presence of two forms of each species. An 'inshore' Bryde's whale is confined to the tropics, whereas a larger 'offshore' form ranges into temperate waters, where it has been recorded as far south as Bass Strait (Dixon and Frigo 1994). Similarly, a diminutive form of minke occurs mainly in the tropical – subtropical region north to at least 12° S, although there are records as far as 58–65° S, while a 'dark shoulder form', *B. bonaerensis*, ranges not quite so far north in winter as the diminutive form (recorded at 21° S), but migrates to the Antarctic ice edge during summer (Bannister *et al.* 1996). Two other migratory rorquals – the fin whale, *B. physalus*, and the sei whale, *B. borealis*, overwinter in subtropical to temperate waters in the Australian region, but they tend to remain well offshore and it is not known whether either species ranges into NT waters (Bannister *et al.* 1996); in any case they rarely strand.

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The Beagle

RECORDS OF THE MUSEUMS AND ART GALLERIES
OF THE NORTHERN TERRITORY

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